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Systematics and biogeography of Chrysogorgiidae from the Indian Ocean: discovery of new species on deep-sea ridges

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Abstract

Species of the family Chrysogorgiidae are distributed worldwide in deep-sea environments. However, most recorded species of this family were from the Atlantic and Pacific Oceans, with only a few reports from the Indian Ocean, particularly from ridge regions. This study describes three new species and reports two known species from Indian Ocean ridges, integrating morphological and molecular analyses (*mtMutS* and *28S rDNA*). *Chrysogorgia pugnioides* Ge, Hu & Xu, **sp. nov.** is characterized by fist-like polyps; warty spindles in tentacles; flat and irregular spindles and elongate scales in the polyp body wall; and slender and smooth scales with toothed to irregular edges in the coenenchyme. *Iridogorgia acutisclerita* Ge, Zhang & Xu, **sp. nov.** resembles *I. splendens* but differs by possessing needles and pointed elongate scales in the polyp body wall. *Iridogorgia levisquama* Ge, Zhang & Xu, **sp. nov.** is differentiated from the congeneric *I. squarrosa* by slender and smooth scales with sharp ends in the polyp body wall and needles with fine wartiness in the tentacles. *Parachrysogorgia chryseis* and *Metallogorgia melanotrichos* are reported as new records for the Indian Ocean ridges. These findings expand the known biodiversity and biogeographic range of Chrysogorgiidae in the Indian Ocean ridges.

Key Words

Carlsberg Ridge, Chrysogorgiidae, Ninetyeast Ridge, phylogeny, taxonomy

Introduction

Chrysogorgiidae Verrill, 1883, is widely distributed globally, with nearly all species restricted to deep-sea habitats (Pante and Watling 2012). The family currently comprises over 100 species in 7 valid genera: *Chrysogorgia* Duchassaing & Michelotti, 1864, *Iridogorgia* Verrill, 1883, *Metallogorgia* Versluys, *Radicipes* Stearns, 1883, 1902, *Parachrysogorgia* Xu, Zhan & Xu, 2023, *Pseudochrysogorgia* Pante & France, 2010, *Ramuligorgia* Cairns, Cordeiro & Xu in Cairns et al. 2021 (McFadden et al. 2025; Xu et al. 2025).

Chrysogorgia is the most speciose genus, containing 69 valid species, distributed across various oceans at depths from 10 m to 4,492 m (Xu et al. 2023). Colonies are usually bottlebrush-shaped, although some species are bi- or multi-flabellate, and others form tree-like colonies with long straight or zigzagging stems (Xu et al. 2020a). Historically, Versluys et al. (1902) divided *Chrysogorgia* species into three groups ("Spiculosae,"

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"Squamosae aberrantes," and "Squamosae typicae") based on sclerites of the polyp body and tentacle, with a fourth group ("Squamosae aberrantes") added by Cordeiro et al. (2015). However, these four groups were artificial constructs for species identification and lacked phylogenetic significance. Untiedt et al. (2021) later identified nine morphological populations based on molecular data, suggesting 11 candidate genera. Recently, Xu et al. (2023) reclassified the genus into 12 morphological groups based on the form and arrangement of sclerites and established the genus *Parachrysogorgia* Xu, Zhan & Xu, 2023. *Parachrysogorgia* currently includes 13 species and differs from *Chrysogorgia* by possessing a bare, sclerite-free area at the base of each tentacle and eight distinct projections beneath tentacles (Xu et al. 2023).

Species of *Iridogorgia* are typical deep-sea organisms, characterized by an upward-spiraling monopodial axis with brilliant iridescence and unbranched branches arising from one side (Verrill 1883). Although *Rhodaniridogorgia* Watling, 2007, was originally distinguished by its wavy axis (Watling 2007), morphological and phylogenetic analyses have since supported its synonymy with *Iridogorgia* (Xu et al. 2021; Xu et al. 2025). Consequently, *I. superba* Nutting, 1908 was restored, and the new combination *I. fragilis* (Watling, 2007) was established (Xu et al. 2021). Presently, the genus *Iridogorgia* comprises 14 valid species: two predominantly found in the North Atlantic, nine restricted to the Pacific, and *I. magnispiralis*, *I. fontinalis*, and *I. splendens* found in both oceans (Xu et al. 2025).

Metallogorgia is characterized by a single stem with branchlets forming a sympodial pattern along the stronger branches (Versluys et al. 1902). The genus comprises only four deep-sea species: *M. melanotrichos* (Wright & Studer, 1889), *M. macrospina* Kükenthal, 1919, *M. splendens* (Verrill, 1883), and *M. tenuis* Pasternak, 1981 (Verrill 1883; Wright 1889; Kükenthal 1919; Pasternak 1981). *Metallogorgia melanotrichos* has been recorded in the central Indo-Pacific, western and central Pacific, and Atlantic Ocean (Wright 1889; Xu et al. 2020b), while *M. macrospina* was first described from the Indian Ocean off Sumatra and subsequently found on seamounts in the Western Pacific (Kükenthal 1919; Xu et al. 2020b). *Metallogorgia splendens* and *M. tenuis* are known only from the Atlantic and Western Pacific, respectively (Verrill 1883; Pasternak 1981).

Compared to the Atlantic and Pacific Oceans, the deep-sea corals of the Indian Ocean Ridge system have historically been under-researched. Recently, several new species and records have been described from the central and northern Indian Ocean ridges, belonging to families such as Keratoisididae (Periasamy et al. 2023b), Sarcodictyonidae (Periasamy et al. 2023a), Victorgorgiidae (Periasamy and Ingole 2025), and Coralliidae (Hu et al. 2025). However, the family Chrysogorgiidae remains rarely recorded in the Indian Ocean, particularly along the ridge systems. The lack of taxonomic and genetic data for this family in the Indian Ocean hinders our understanding of its biogeographic distribution and phylogeny, limiting insights into the connectivity between Indian Ocean populations and those in other oceans.

We conducted a deep-sea biological survey of the Carlsberg Ridge and Ninetyeast Ridge in the Indian Ocean and collected 13 Chrysogorgiidae specimens in 2022. This study integrates morphological and molecular analyses to describe one new species of *Chrysogorgia* and two new species of *Iridogorgia* and report two known species for *Parachrysogorgia* and *Metallogorgia*. Our objectives are to (1) expand the known biogeographic ranges of Chrysogorgiidae in the Indian Ocean, and (2) contribute new insights into the diversity and evolution of these corals in deep-sea ridge environments.

Materials and methods

Specimen collection and morphological examination

Specimens of Chrysogorgiidae were collected from the Indian Ocean using the HOV *JiaoLong* launched from R/V *ShenHai YiHao* during the DY72 cruise in 2022. Two specimens were collected from the Carlsberg Ridge, and the remaining 11 were from the Ninetyeast Ridge (Fig. 1). All specimens were photographed *in situ* and on board before being preserved in 75% ethanol. These specimens are securely stored at the Marine Ecology Research Center, First Institute of Oceanography, MNR, China.

A stereo dissecting microscope (Nikon SMZ1270) was used to examine the overall morphology and anatomical structures of the colonies and polyps. Sclerites from different parts of the polyps and coenenchyme were isolated by digesting the tissues in a 10% sodium hypochlorite solution, then rinsed repeatedly with deionized water. Whole polyps and sclerites were mounted on double-sided insulating tape, dried, and gold-coated. Their microstructures were subsequently examined using a Regulus 8100 scanning electron microscope (SEM).

DNA extraction and sequencing

Total genomic DNA was extracted from polyps using the MicroElute Genomic DNA Kit (OMEGA, USA). The partial mitochondrial mutS homolog (*mtMutS*) and nuclear 28S ribosomal DNA (*28S rDNA*) regions were amplified by polymerase chain reaction (PCR) for phylogenetic analysis. PCR amplification was performed using the primer pairs AnthoCorMSH (Herrera et al. 2010) and Mut-3458R (Sánchez et al. 2003) for *mtMutS*, and 28S-Far and 28S-Rar (McFadden and van Ofwegen 2013) for *28S rDNA*. PCR amplifications and sequencing of the markers followed (Hu et al. 2025).

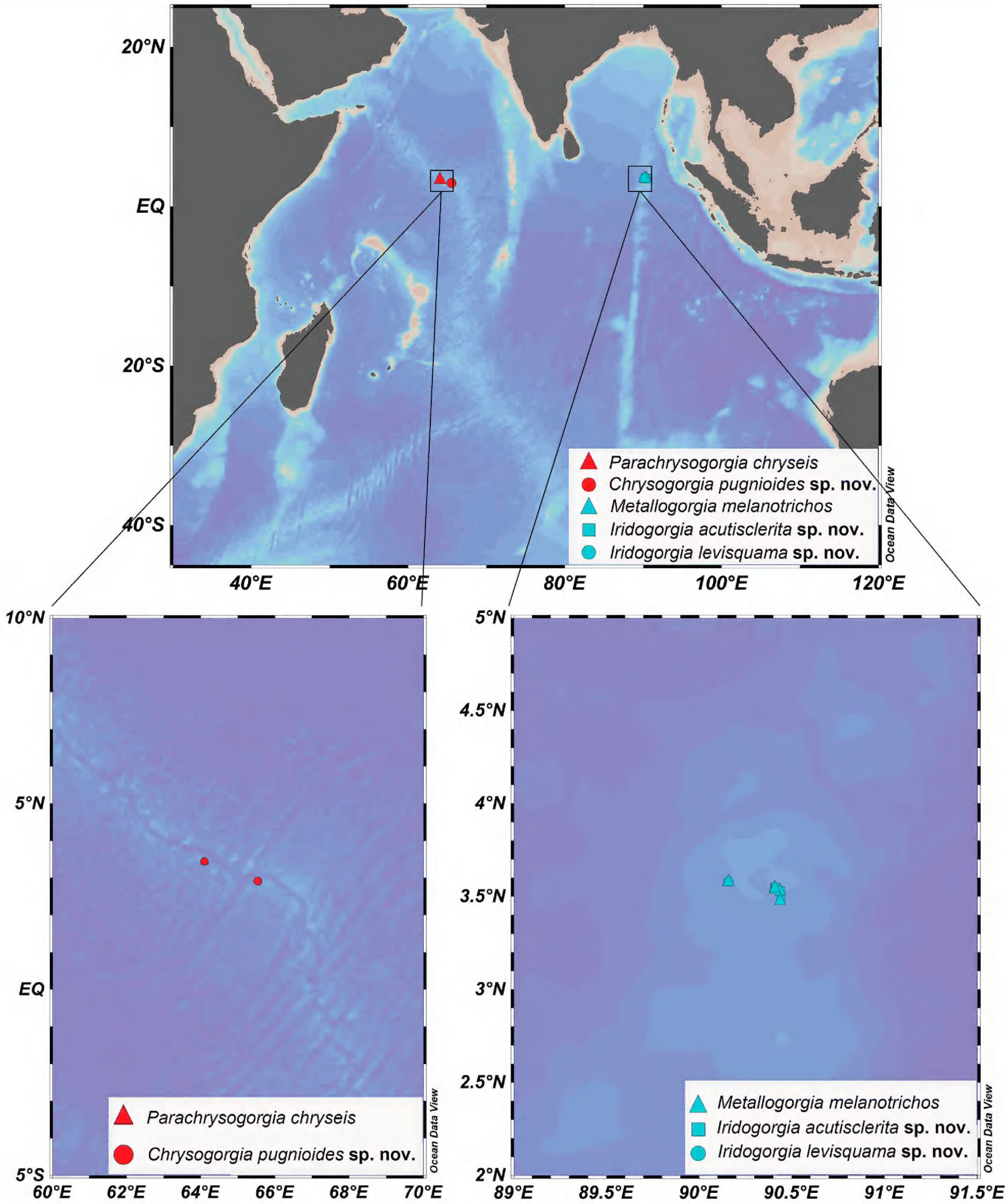

Figure 1. The map shows the collection sites of five species from the Indian Ocean. Red circles and triangles indicate *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. and *Parachrysogorgia chryseis*, respectively, from the Carlsberg Ridge. Cyan circles, rectangles, and triangles represent *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov., *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov., and *Metallogorgia melanotrichos*, respectively, from the Ninetyeast Ridge.

Genetic distance and phylogenetic analyses

All available *mtMutS* and *28S rDNA* sequences of Chrysogorgiidae were used for genetic distance analyses, with sequences from undetermined and duplicate species excluded. Nucleotide sequences were aligned with default parameters in MAFFT v7.313 (Katoh and Standley 2013), with protein-coding genes optimized using

MACSE v2.03 (Ranwez et al. 2018). The sequences were then trimmed to conserved blocks using Gblocks v0.91b (Talavera and Castresana 2007). Genetic distances for single loci, both within and between species of these four genera, were calculated as uncorrected '*p*' distances using MEGA 11 (Tamura et al. 2021).

Phylogenetic trees were constructed using both *mtMutS* and *28S rDNA* datasets. The *mtMutS* dataset comprised 85 Chrysogorgiidae sequences, with three Keratoisididae sequences as outgroups (Table 1, Suppl. material 1: table S1). The *28S rDNA* dataset comprised 58 Chrysogorgiidae sequences, with two Keratoisididae sequences as outgroups (Table 1, Suppl. material 1: table S1). The phylogenetic trees were generated using the maximum likelihood (ML) and Bayesian inference (BI) algorithms. ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the best-fit model using the BIC criterion. For the ML analyses, the best-fit models were TVM+F+G4 for *mtMutS* and TN+F+G4 for *28S rDNA*. For the BI analyses, GTR+F+G4 and HKY+F+G4 were selected for *mtMutS* and *28S rDNA*, respectively. ML trees were constructed using IQ-TREE v1.6.8 (Nguyen et al. 2015) with 10,000 standard bootstrap replicates. BI trees were generated using MrBayes v3.2.6 (Revell 2012), with posterior probabilities estimated from 10,000,000 Markov chain Monte Carlo (MCMC) generations across four chains, sampling every 1,000 generations and discarding the first 25% as burn-in.

Results

Taxonomy

Phylum Cnidaria Hatschek, 1888
Subphylum Anthozoa Ehrenberg, 1834
Class Octocorallia Haeckel, 1866
Order Scleralcyonacea McFadden, van Ofwegen & Quattrini, 2022
Family Chrysogorgiidae Verrill, 1883
Genus *Chrysogorgia* Duchassaing & Michelotti, 1864

Chrysogorgia pugnioides Ge, Hu & Xu, sp. nov.

https://zoobank.org/4E82B5AF-8DA7-4A96-8664-A3CF786BCBE8

Figs 2–5

Material examined. ***Holotype*:** FIO-IND72-JL-BEN22107, Guangde Ridge, the northern Indian Ocean, 2.91°N, 65.54°E, 2,674 m, collected on 15 June 2022.

Diagnosis. *Chrysogorgia* with bottlebrush-shaped colony and 1/3R–2/5R branching sequence. Polyps fist-like. Sclerites with irregular edges. Spindles warty with two pointed ends in tentacle rachis. Similar spindles in the upper polyp body wall but a little flat and more irregular. Flat spindles to elongate scales in the basal polyp body wall. Slender and smooth scales in coenenchyme.

Description. ***Colony*.** Holotype bottlebrush-shaped with a slightly curved main stem, approximately 58 cm long and 20 cm wide in maximum (Fig. 2B). Holdfast disc-shaped *in situ* but not recovered after collection (Fig. 2A). Stem approximately 4 mm in diameter at base, brown with aeruginous metallic luster. Branching sequence 1/3R–2/5R (Fig. 2B). Branches subdivided dichotomously, up to eight orders with branching angle 60°–80°. Distances between adjacent branches 2–6 mm, orthostiche intervals 10–12 mm, the first internode of branch 16–24 mm and terminal branchlets 5–6 mm long (Fig. 2B).

***Polyp*.** Polyps fist-like, expanded distally, 1.3–2.0 mm tall and 1.2–1.7 mm wide (Fig. 2D–G). Tentacles contracted but not completely retracted. Polyps arranged 0 to four on first internode, one and rarely two in middle internodes, and one or two in the terminal branchlets (Fig. 2B, C). Polyps absent on the stem. Verrucae absent.

***Sclerites*.** Small scales in pinnules flat and elongate with irregular edges and two finely serrated ends, measuring 126–142 μm long by 37–50 μm wide (Fig. 3B). Spindles in tentacle rachis usually longitudinally arranged with two narrow to pointed ends and dense warts, some of them with irregular edges and slightly curved, measuring 291–565 μm long by 61–118 μm wide (Fig. 3A).

Table 1. Specimen location and genetic data obtained in this study.

Species	Voucher number	Location	GenBank accession	
			mtMutS	*28S rDNA*
Chrysogorgia pugnioides sp. nov.	FIO-IND72-JLBEN22107	Guangde Ridge, Indian Ocean	PV341126	PX687963
Iridogorgia acutisclerita sp. nov.	FIO-IND72-JLBEN22309	Ninetyeast Ridge, Indian Ocean	PV341128	PX687964
Iridogorgia acutisclerita sp. nov.	FIO-IND72-JLBEN22402	Ninetyeast Ridge, Indian Ocean	PV341129	PX687965
Iridogorgia acutisclerita sp. nov.	FIO-IND72-JLBEN22404	Ninetyeast Ridge, Indian Ocean	PV341130	PX687966
Iridogorgia acutisclerita sp. nov.	FIO-IND72-JLBEN22511	Ninetyeast Ridge, Indian Ocean	PV341131	PX687967
Iridogorgia levisquama sp. nov.	FIO-IND72-JLBEN22604	Ninetyeast Ridge, Indian Ocean	PV341133	PX687968
Metallogorgia melanotrichos	FIO-IND72-JLBEN22605	Ninetyeast Ridge, Indian Ocean	PV341141	PX687973
Metallogorgia melanotrichos	FIO-IND72-JLBEN22301	Ninetyeast Ridge, Indian Ocean	PV341135	PX687969
Metallogorgia melanotrichos	FIO-IND72-JLBEN22310	Ninetyeast Ridge, Indian Ocean	PV341136	–
Metallogorgia melanotrichos	FIO-IND72-JLBEN22306	Ninetyeast Ridge, Indian Ocean	PV341137	PX687971
Metallogorgia melanotrichos	FIO-IND72-JLBEN22401	Ninetyeast Ridge, Indian Ocean	PV341138	–
Metallogorgia melanotrichos	FIO-IND72-JLBEN22510	Ninetyeast Ridge, Indian Ocean	PV341139	PX687972
Parachrysogorgia chryseis	FIO-IND72-JLBEN22006	Carlsberg Ridge, Indian Ocean	PV341125	PX687962

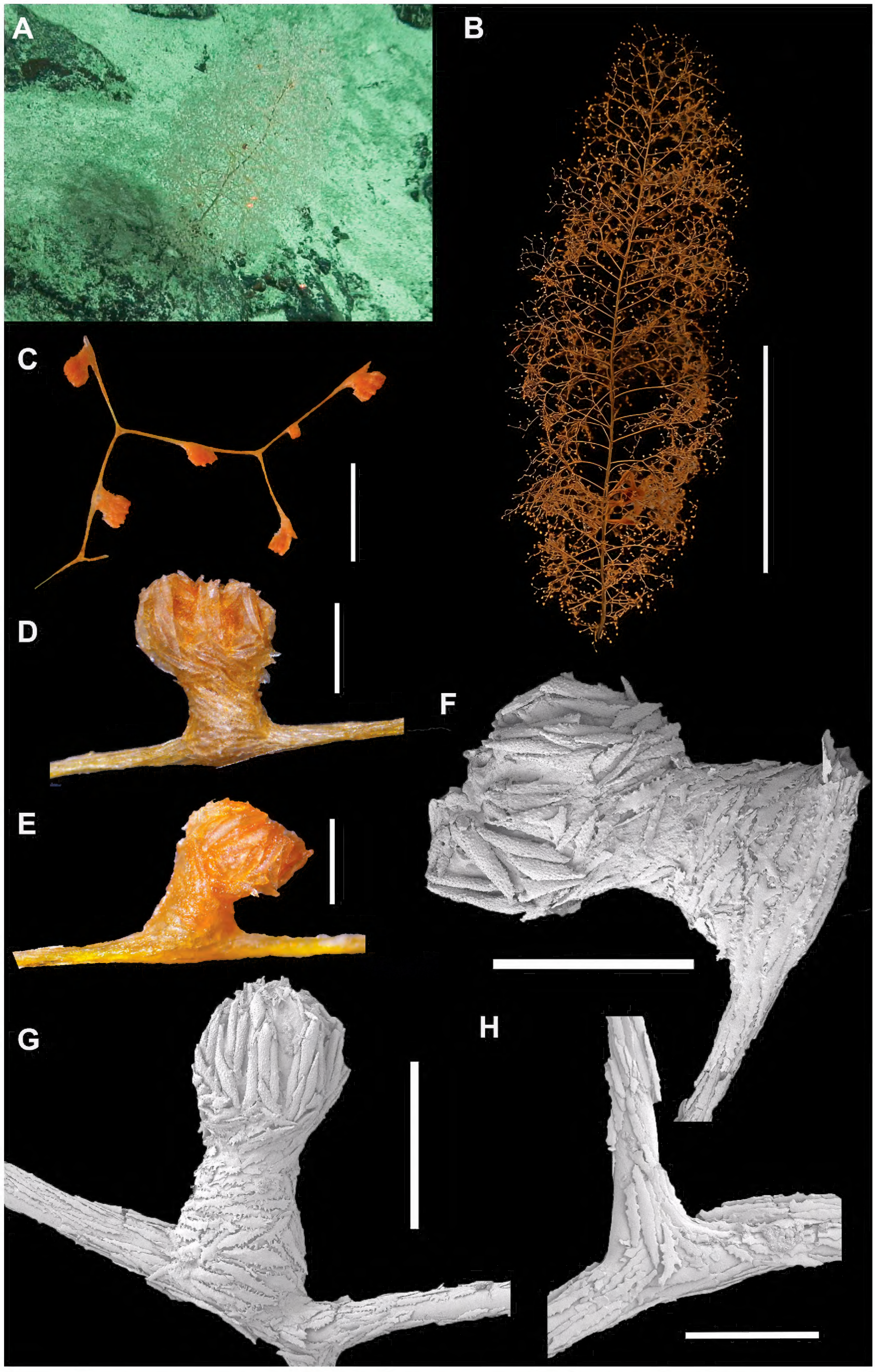

Figure 2. The external morphology and polyps of *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. **A**, **B.** The holotype *in situ* and after collection; **C.** The partial branch morphology; **D–E.** Single polyps under a light microscope; **F–G.** Single polyps under SEM; **H.** A part of the branch under SEM. Scale bars: 10 cm (**B**); 5 mm (**C**); 1 mm (**D–H**).

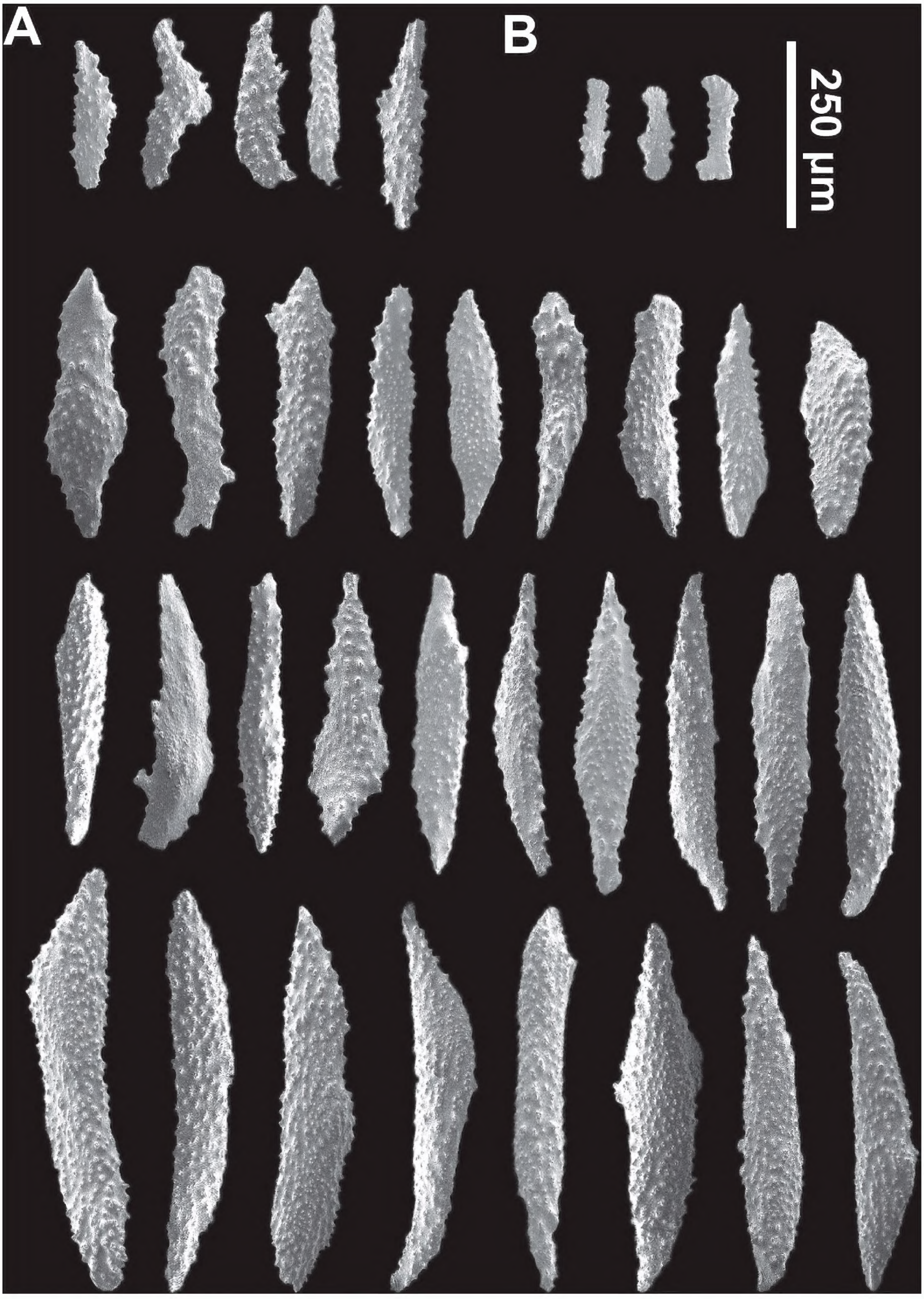

Figure 3. Sclerites in the tentacles of *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. **A.** Sclerites in the tentacle rachis; **B.** Sclerites in the pinnule.

Spindles in the upper polyp body wall obliquely or transversely arranged, a little flat with abundant warts and more irregular edges, some branched or crossed, measuring 283–512 μm long by 71–324 μm wide (Fig. 4A). Flat spindles to elongate scales in basal polyp body wall transversely or obliquely arranged, with toothed to extremely irregular edges, nearly smooth or with sparse warts, measuring 286–453 μm long by 56–99 μm wide (Fig. 4B). Slender scales in coenenchyme arranged along to the branches, nearly smooth with toothed to irregular edges, measuring 130–413 μm long by 27–72 μm wide (Fig. 5).

Type locality. Guangde Ridge in the northern Indian Ocean with depth of 2,674 m.

Etymology. The Latin adjective *pugnioides* means "fist-shaped" referring to the polyp morphology resembling a clenched fist, particularly in the contracted state of its tentacles.

Distribution and habitat. Found from the Guangde Ridge in the northern Indian Ocean with water depth of 2,674 m.

Remarks. *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. belongs to Xu's group B2, with spindles in the tentacle rachis and upper part of the polyp body wall and scales in the lower part of the body wall. *C. pugnioides* sp. nov. and *C. agassizii* (Group B2) both exhibit a 2/5R branching sequence but differ in having warty spindles and nearly smooth scales with irregular margins in both the polyp body wall and the coenenchyme (vs. scales with smooth to finely granular faces, finely serrate margins, and rounded distal ends). *C. pugnioides* sp. nov. is also similar to *C. ramificans* Xu, Li, Zhan & Xu, 2019, in colony form and branching sequence but differs by obviously different sclerites in the basal polyp body wall: the former has flat spindles to elongate scales with toothed to irregular edges, while the latter has rather stout and regular rods and spindles.

Genus *Parachrysogorgia* Xu, Zhan & Xu, 2023

Parachrysogorgia chryseis (Bayer & Stefani, 1988)

Figs 6–9

Chrysogorgia chryseis Bayer & Stefani, 1988: 267–269, Figs 7, 8.

Parachrysogorgia chryseis (Bayer & Stefani, 1988): Xu et al. 2023: 20–35, Figs 3–16.

Material examined. Specimen FIO-IND72-JLBEN22006, Carlsberg Ridge, the northern Indian Ocean, 64.10°E, 3.44°N, 1,700 m, collected on 13 June 2022.

Description. ***Colony.*** Specimen FIO-IND72-JLBEN22006 *in situ* grew on the white branch of a dead coral (Fig. 6A). Colony bi-flabellate, approximately 20 cm high and 22 cm wide. Major branches of each fan subdivide dichotomously and sympodially, with bifurcation angles reaching up to 90°, forming a dense branching pattern (Fig. 6B). Colony yellow after collection, with a golden-yellow axis.

Polyp. Polyps contracted, narrower than head and base, measuring 1.8–3.3 mm in height and 1.2–1.7 mm in width. Tentacles contracted but not fully retracted. Sclerites forming conspicuous sharp points at base of naked tract below each tentacle. Polyps octagonal in apical view with concave edges (Fig. 6E, G, I). Verrucae present on some branches (Fig. 6F).

Sclerites. Scales in pinnules slender, some curved and gutter-like, measuring 271–320 μm long by 30–68 μm wide (Fig. 7C). Scales in the upper part of tentacles transversely arranged, lobed with irregular shape, nearly smooth or with few warts, measuring 147–245 μm long by 48–115 μm wide (Fig. 7A). Rods and scales in the basal part of tentacles longitudinally arranged, thick with irregular edges and shape, coarse with many warts on surface, measuring 174–314 μm long by 16–74 μm wide (Fig. 7B). Scales forming the points smooth and slender, usually with irregular edges, some of them curved or branched, measuring 313–650 μm long by 55–134 μm wide (Fig. 7D). Scales in polyp body wall obliquely or transversely arranged, smooth, usually with a medial constriction or irregular lobed edges, measuring 132–473 μm long by 63–162 μm wide (Fig. 8). Similar scales in coenenchyme smooth and elongate with medial constriction or irregular lobed edges, occasionally crossed or forked, measuring 67–239 μm long by 28–60 μm wide (Fig. 9).

Distribution and habitat. Pacific Ocean, including the Indonesian Ceram Sea, 732 m (Bayer and Stefani 1988), and seamounts on the Caroline Ridge, 688–1692 m (Xu et al. 2023). The Carlsberg Ridge in the northern Indian Ocean with water depths of 1,700 m.

Remarks. Specimen FIO-IND72-JLBEN22006 is consistent with *Parachrysogorgia chryseis* in having a bi-flabellate colony, eight distinct projections beneath the tentacles, a bare, sclerite-free area at the base of each tentacle, and similar sclerite forms (smooth scales with medial constriction or irregular shape in the polyp body wall and coenenchyme; lobed rods and scales in the tentacles). Specimen FIO-IND72-JLBEN22006 differs from specimens from the Pacific Ocean by the presence of verrucae on some branches, with scales and rods in the tentacles being smoother and lacking large wart.

Genus *Iridogorgia* Verrill, 1883

Iridogorgia acutisclerita Ge, Zhang & Xu, sp. nov.

https://zoobank.org/2B7783AC-FFBA-4427-BB12-29780FFE385B

Figs 10–12

Material examined. ***Holotype*:** FIO-IND72-JLBEN22309, Ninetyeast Ridge, 3.55°N, 90.41°E, 1,962 m, collected on 27 June 2022. ***Paratype*:** FIO-IND72-JLBEN22402, Ninetyeast Ridge, 3.53°N, 90.44°E, 1,977 m, collected on 28 June 2022. FIO-IND72-JLBEN22404, 3.55°N, 90.4122°E, 1,962 m, collected on 28 June 2022. FIO-IND72-JLBEN22511, 3.48°N, 90.44°E, 1,897 m, collected on 29 June 2022.

Diagnosis. Colony with closely coiled helices. Polyps and branches with abundant verrucae. Rods sparse at the basal of tentacle rachis. Needles and a few elongate scales

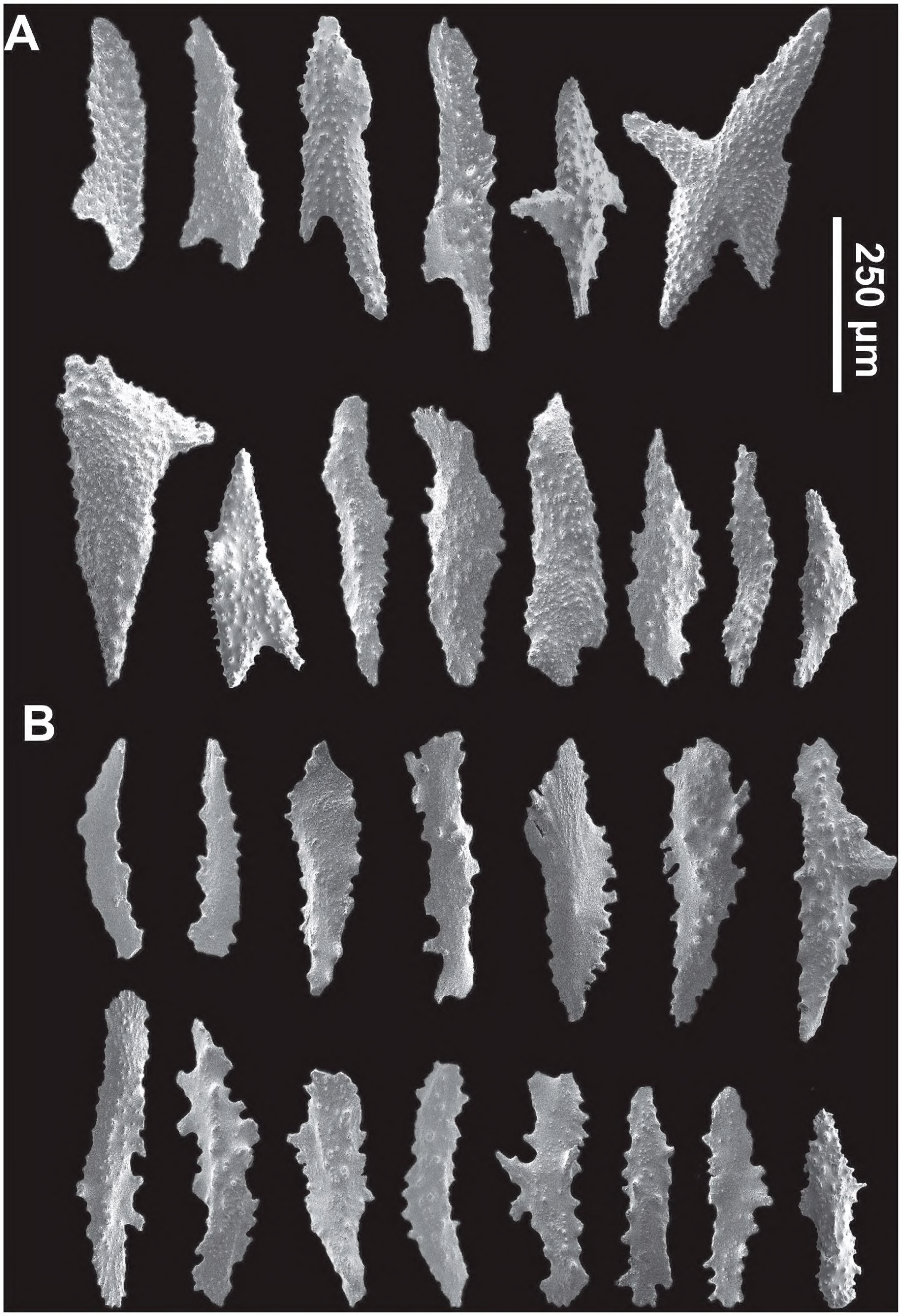

Figure 4. Sclerites in the polyp body wall of *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. **A.** Sclerites at the upper part of the body wall; **B.** Sclerites at the basal part of the body wall.

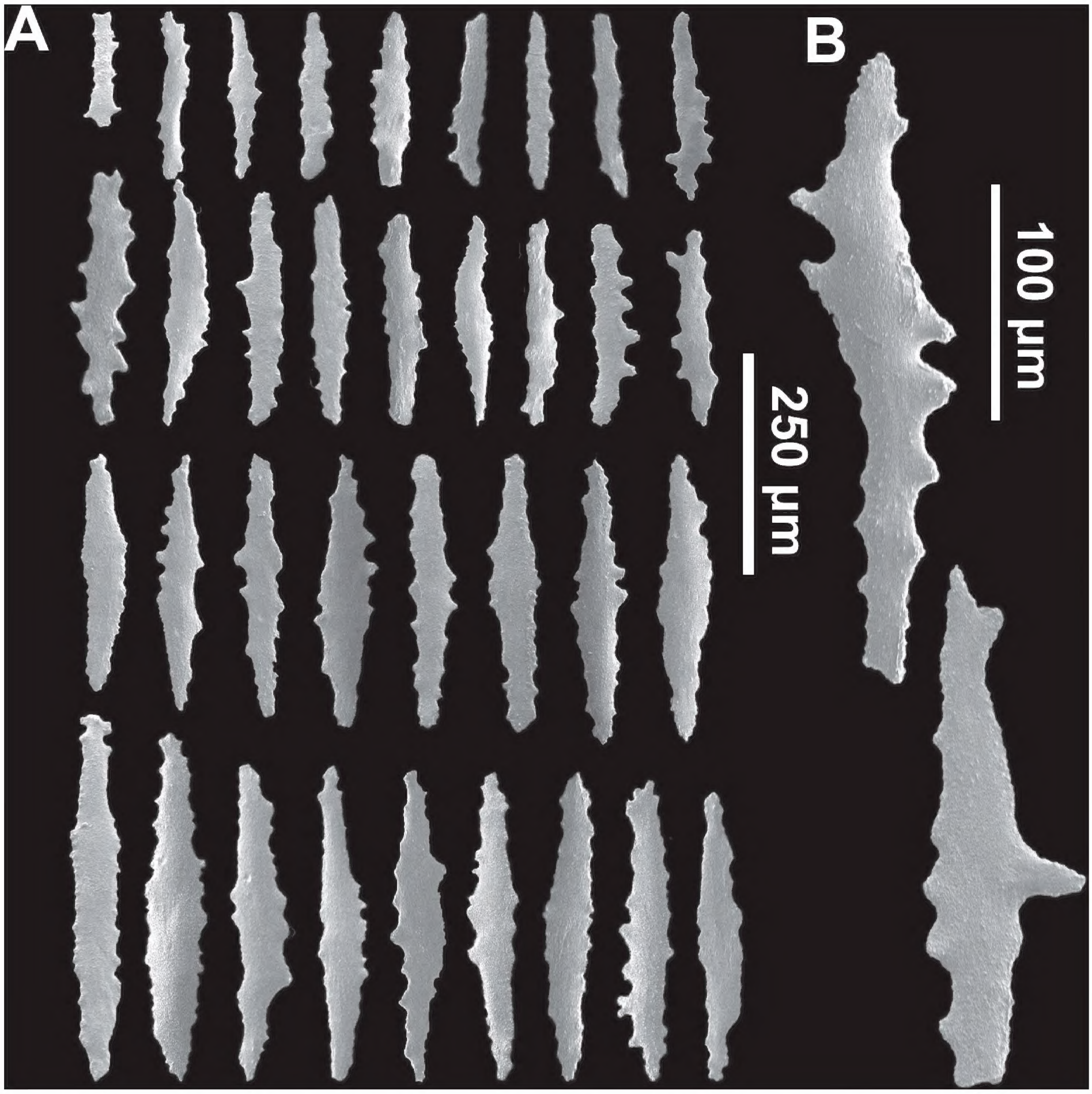

Figure 5. Sclerites in the coenenchyme of *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. **A.** Sclerites in the coenenchyme; **B.** Close-up of sclerites in the coenenchyme.

with two pointed ends in the polyp body wall. Slender needles in coenenchyme.

Description. ***Colony.*** Holotype *in situ* attached to the hard chalk substrate (Fig. 10A). Colony approximately 73 cm in height with the holdfast not recovered after collection. The direction of growth clockwise. The central axis composed of 12 helical turns with each turn approximately 6 cm in height and 2 cm in diameter (Fig. 10C). Branches slender and slightly arc-shaped, up to 17 cm long, arising sequentially along one side of the central axis from the sixth helix, approximately 4 mm apart.

Polyp. Polyps short with an expanded body base, approximately 1.5 mm in height and 2.5–3.5 mm in width (Fig. 10F, G). When tentacles fully extended, the polyps up to 3.7 mm in height. Polyps arranged along one side of the branches, spaced 3–7 mm apart, averaging 6 mm. Verrucae abundant on the basal parts of the polyp body and along the branches (Fig. 10I, K).

Sclerites. Rods in tentacle rachis longitudinally arranged, sparse with abundant warts, occasionally with shallow cracks on surface, measuring 281–294 μm long by 31–38 μm wide (Fig. 11B). Needles and a few elongate scales in the polyp body wall transversely or obliquely arranged, usually with two sharp ends and some fine warts on surfaces, some of them with a slightly medial constriction, measuring 184–453 μm long by 26–50 μm wide (Figs 11A, 12A). Needles arranged along the branches, slender with two pointed ends and dense fine warts on surface, measuring 257–770 μm long by 42–50 μm wide (Figs 11C, 12B).

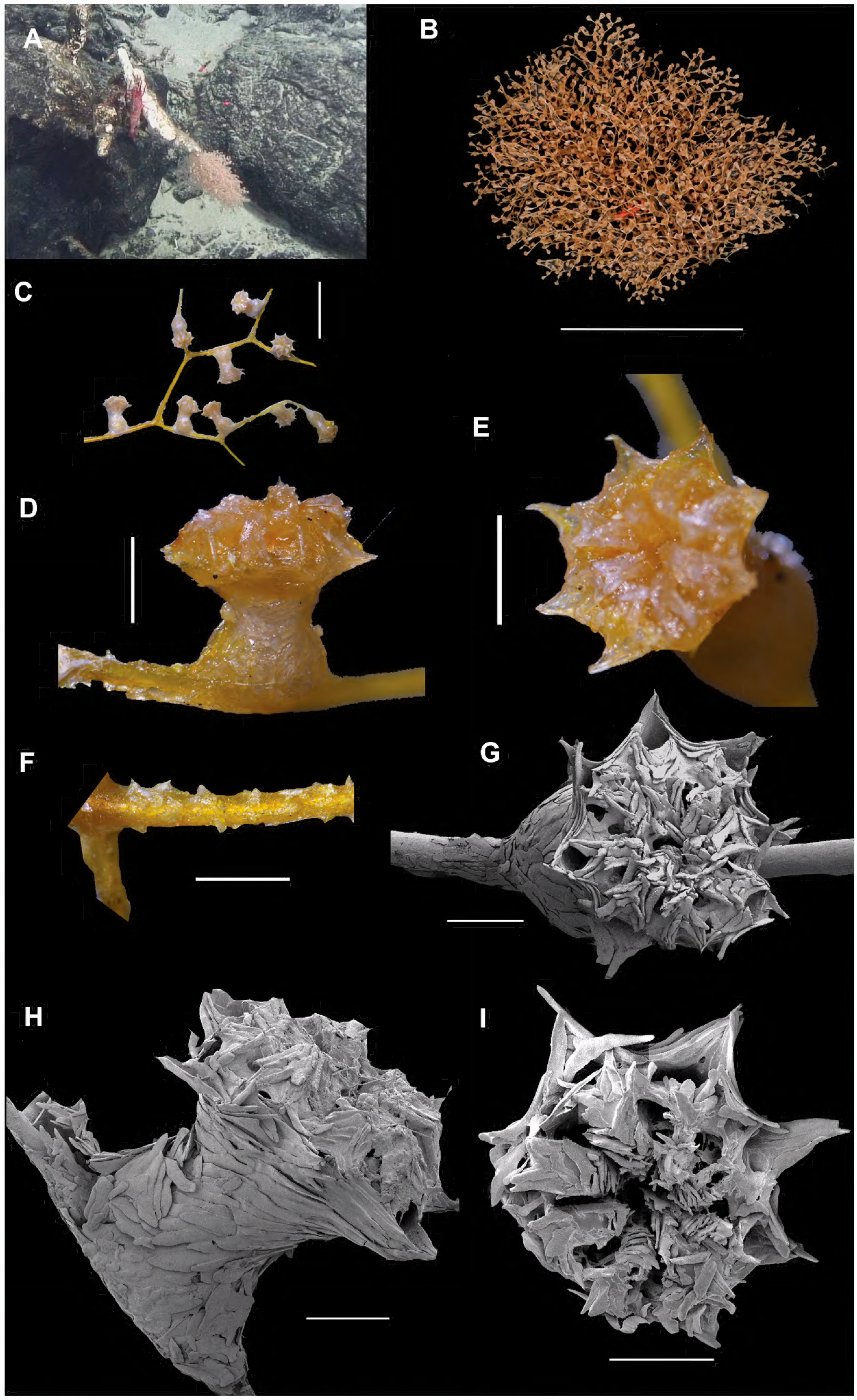

Figure 6. The external morphology and polyps of *Parachrysogorgia chryseis* Bayer & Stefani, 1988, specimen FIO-IND72-JL-BEN22006. **A**, **B.** Specimen *in situ* and after collection; **C.** A part of the branch under a light microscope; **D**, **E.** Single polyps under a light microscope; **F.** A part of the branch under a light microscope; **G–I.** Single polyps under SEM. Scale bars: 10 cm (**B**); 5 mm (**C**); 1 mm (**D–F**); 500 μm (**G–I**).

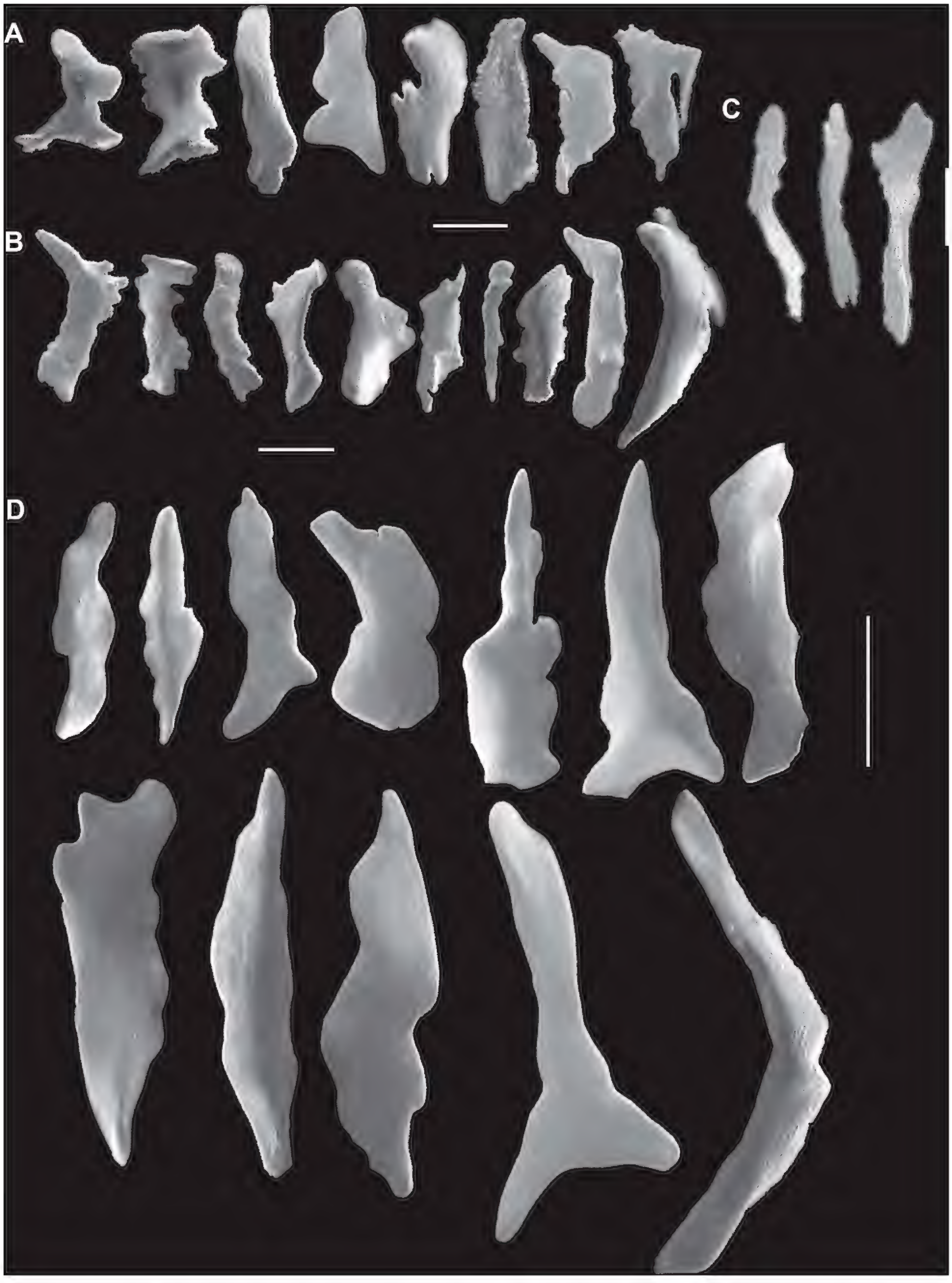

Figure 7. Sclerites in the tentacles of *Parachrysogorgia chryseis* Bayer & Stefani, 1988. **A.** Sclerites in the upper part of the tentacle rachis; **B.** Sclerites in the basal part of the tentacle rachis; **C.** Sclerites in the pinnules; **D.** Sclerites from the connecting region between the bases of every two tentacles. Scale bars: 100 μm (**A–D**).

Figure 8. Sclerites in the polyp body wall of *Parachrysogorgia chryseis* Bayer & Stefani, 1988.

Variation of paratypes. Paratype FIO-IND72-JLBEN22402 approximately 71 cm in height, with 12 helical turns, each 5 cm in height and 1.5 cm in diameter; branches originate from the fifth helix upward (Fig. 10B, D). Paratype FIO-IND72-JLBEN22511 approximately 80 cm in height, with white holdfast (Fig. 10E). The central axis comprises 18 helical turns, each 4 cm in height and 1.5 cm in diameter. Branches arise at eighth helixes.

Type locality. Ninetyeast Ridge in the northern Indian Ocean with depth of 1,897–1,977 m.

Etymology. The species name *acutisclerita* is a compound adjective derived from the Latin *acutus*

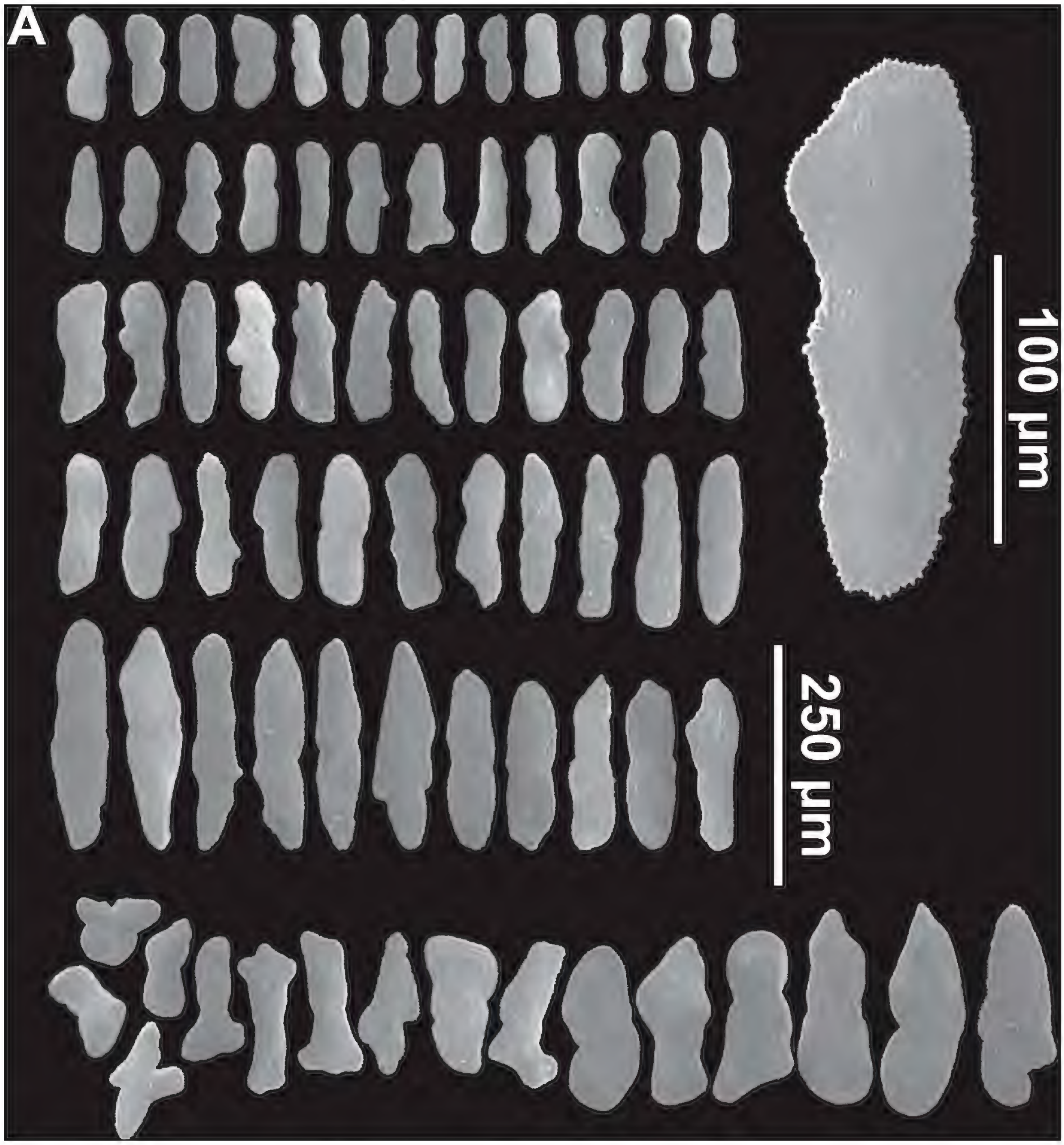

Figure 9. Sclerites in the coenenchyme of *Parachrysogorgia chryseis* Bayer & Stefani, 1988.

(sharp) and the Greek *skleros* (hard, referring to sclerites), referring to the characteristic sclerites, which all feature two sharp ends.

Distribution and habitat. Found from the Ninetyeast Ridge in the northern Indian Ocean with water depths of 1,897–1,977 m. Colony attached to a chalk substrate.

Remarks. *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. is similar to *I. splendens* in colony form and close helical turns but differs from it in having needles and a few elongate scales with two pointed ends in the polyp body wall (vs. needles and rods with relatively rounded ends).

***Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov.**

https://zoobank.org/CF417526-8818-4557-931B-A7C7A372156B

Figs 13, 14

Material examined. ***Holotype*:** FIO-IND72-JL-BEN22604, Ninetyeast Ridge, 3.58°N, 90.16°E, 2,073 m, collected on 30 June 2022.

Diagnosis. Colony with loosely coiled helices. Polyps conical with expanded body base. Sclerites all slender with pointed to sharp ends. Needles in tentacles with fine warts. Scales in polyp body wall nearly smooth with slightly medial constriction and often irregular edges. Abundant needles in coenenchyme.

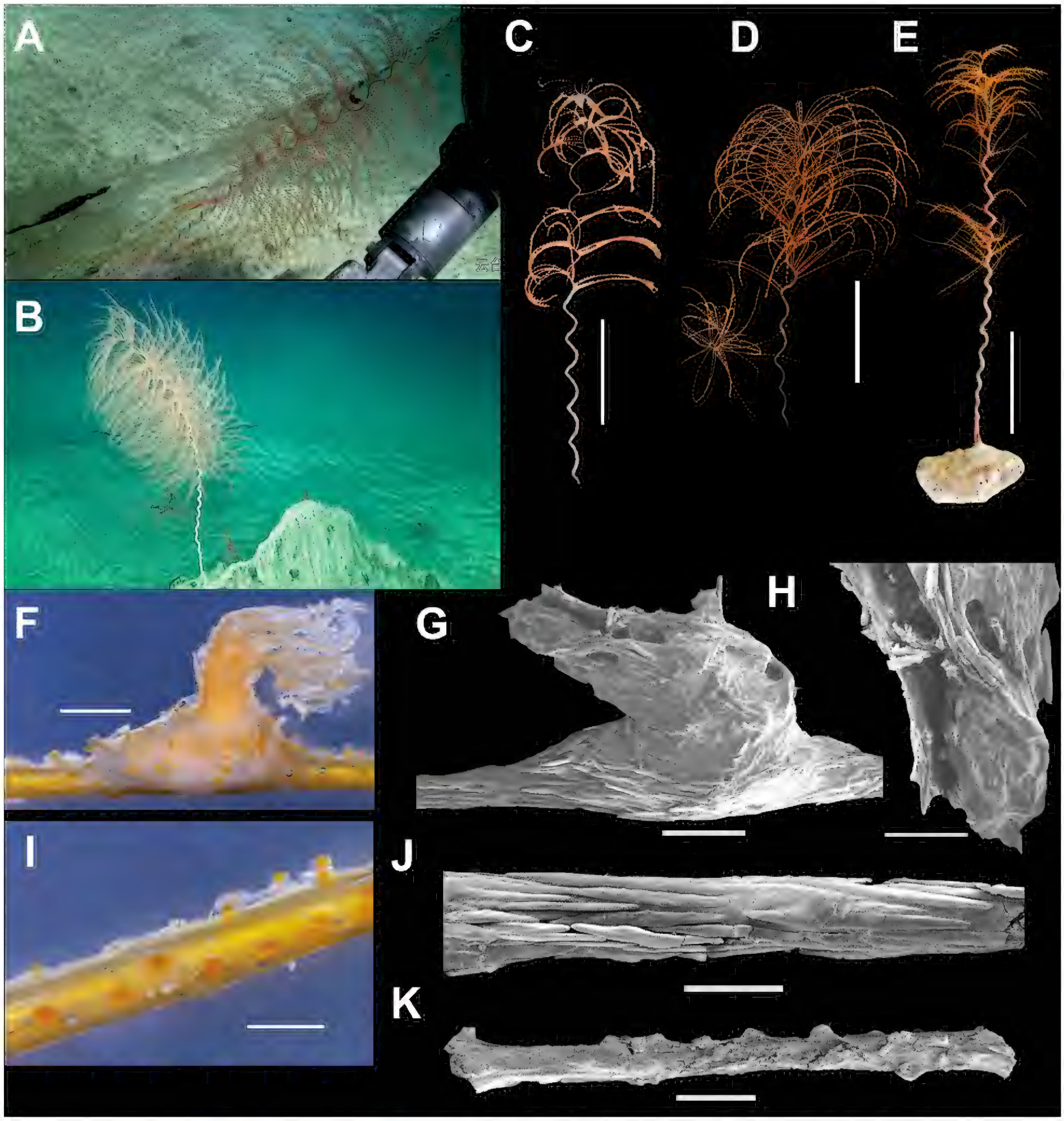

Figure 10. The external morphology of *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. **A.** Holotype FIO-IND72-JLBEN22309 *in situ*; **B.** Paratype FIO-IND72-JLBEN22402 *in situ*; **C–E.** Holotype FIO-IND72-JLBEN22309, paratype FIO-IND72-JLBEN22402, and FIO-IND72-JLBEN225511 after collection; **F.** Single polyp under a light microscope; **G.** Single polyp under SEM; **H.** A part of the tentacle under SEM; **I.** A part of the branch under a light microscope; **J.** A part of the branch with epidermal tissue removed under SEM; **K.** A part of the branch with epidermal tissue under SEM. Scale bars: 20 cm (**C–E**); 1 mm (**F, I**); 500 μm (**G, K**); 250 μm (**H, J**).

Description. ***Colony.*** Holotype *in situ* grew on hard chalk substrate (Fig. 13A). Colony approximately 120 cm in height with a calcareous holdfast approximately 6.5 cm in diameter (Fig. 13B). The direction of growth counterclockwise. The central axis composed of six loosely helical turns, each turn 18 cm in height and 3.5 cm in diameter. Axis approximately 5 mm in diameter at base, with dark iridescent metallic luster. Branches arising approximately 25 cm from base, along one side of the axis, spaced 4–5 mm apart, up to 35 cm long with 32 polyps counted.

Polyps. Polyps conical with expanded body base, approximately 3–4 mm in height. Contracted tentacle width 1.3–1.6 mm and expanded body width 4–4.5 mm (Fig. 13D, E). Polyps slightly inclined along the branch, spaced 3–4 mm apart (Fig. 13C). Tentacles form eight distinct columns extending to the bottom of polyp, up to 3 mm long. Verrucae absent.

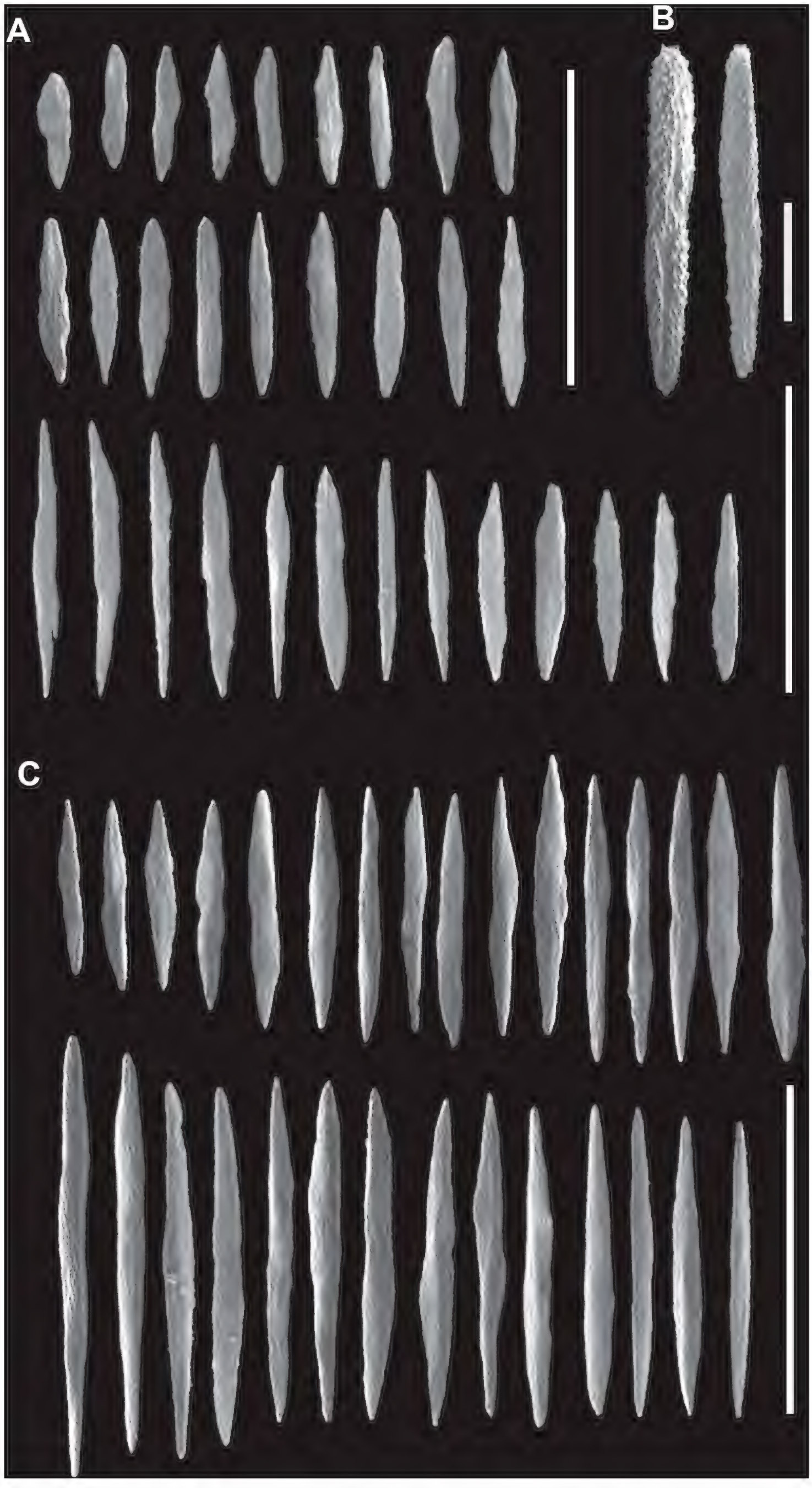

Figure 11. Sclerites of *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov., holotype FIO-IND72-JLBEN22309. **A.** Sclerites in the polyp body wall; **B.** Sclerites in the tentacles; **C.** Sclerites in the coenenchyme. Scale bars: 100 μm (**A**); 500 μm (**B, C**).

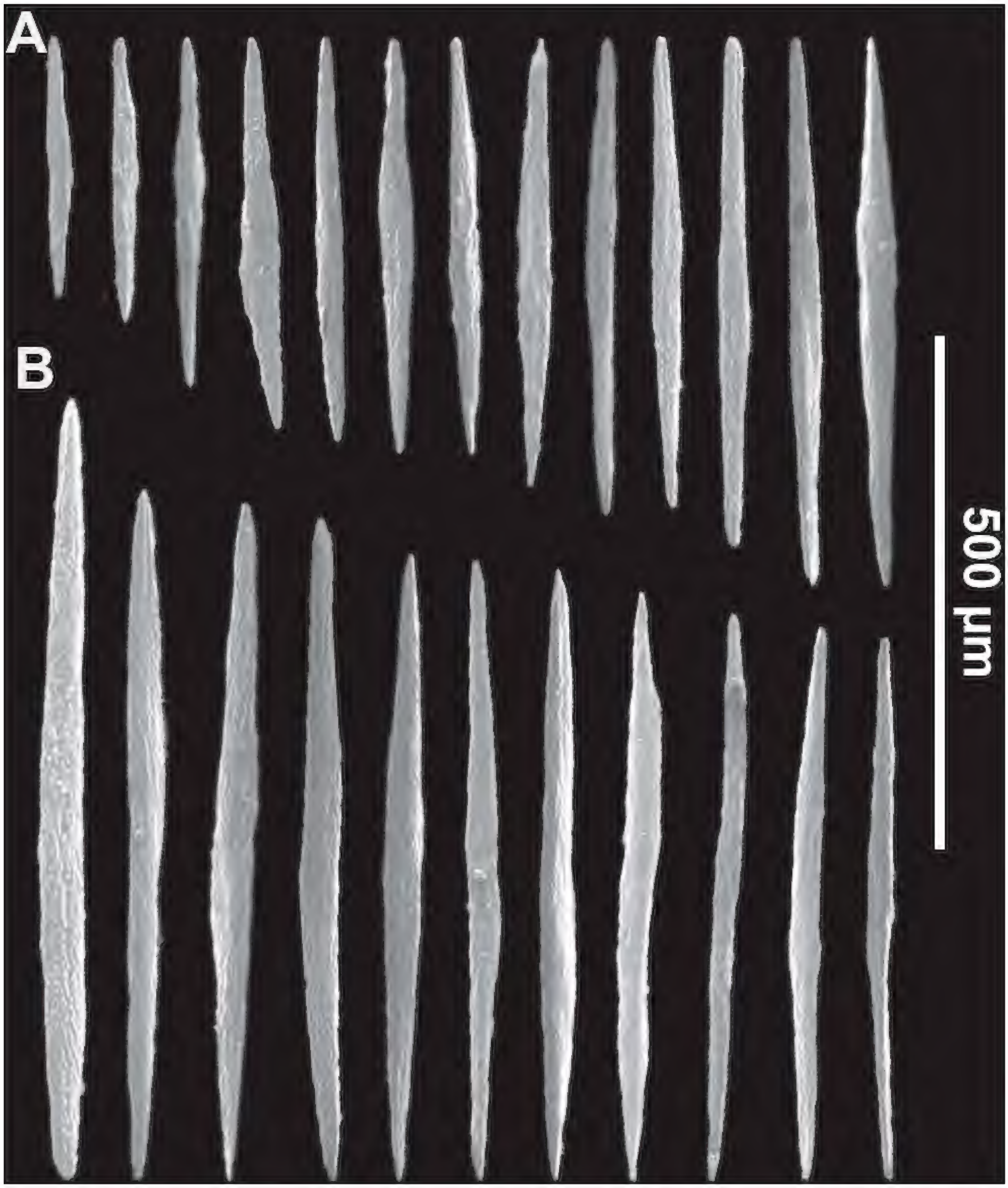

Figure 12. Sclerites in the basal part of **A** polyp body wall and **B** coenenchyme of *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov., paratype FIO-IND72-JLBEN22402.

Sclerites. Needles in tentacles longitudinally arranged, slender with many fine warts and two pointed ends, measuring 395–567 μm long by 29–49 μm wide (Fig. 14A). Elongated to slender scales in polyp body wall transversely or obliquely arranged, nearly smooth with slightly medial constriction and often irregular edges, some of them with large irregular sculpture on surface, measuring 322–756 μm long by 44–83 μm wide (Fig. 14B). Needles in coenenchyme arranged along the branches, slender with fine warts and two sharp ends, occasionally crossed, measuring 318–1355 μm long by 29–83 μm wide (Fig. 14C).

Type locality. Ninetyeast Ridge in the northern Indian Ocean with depth of 2,073 m.

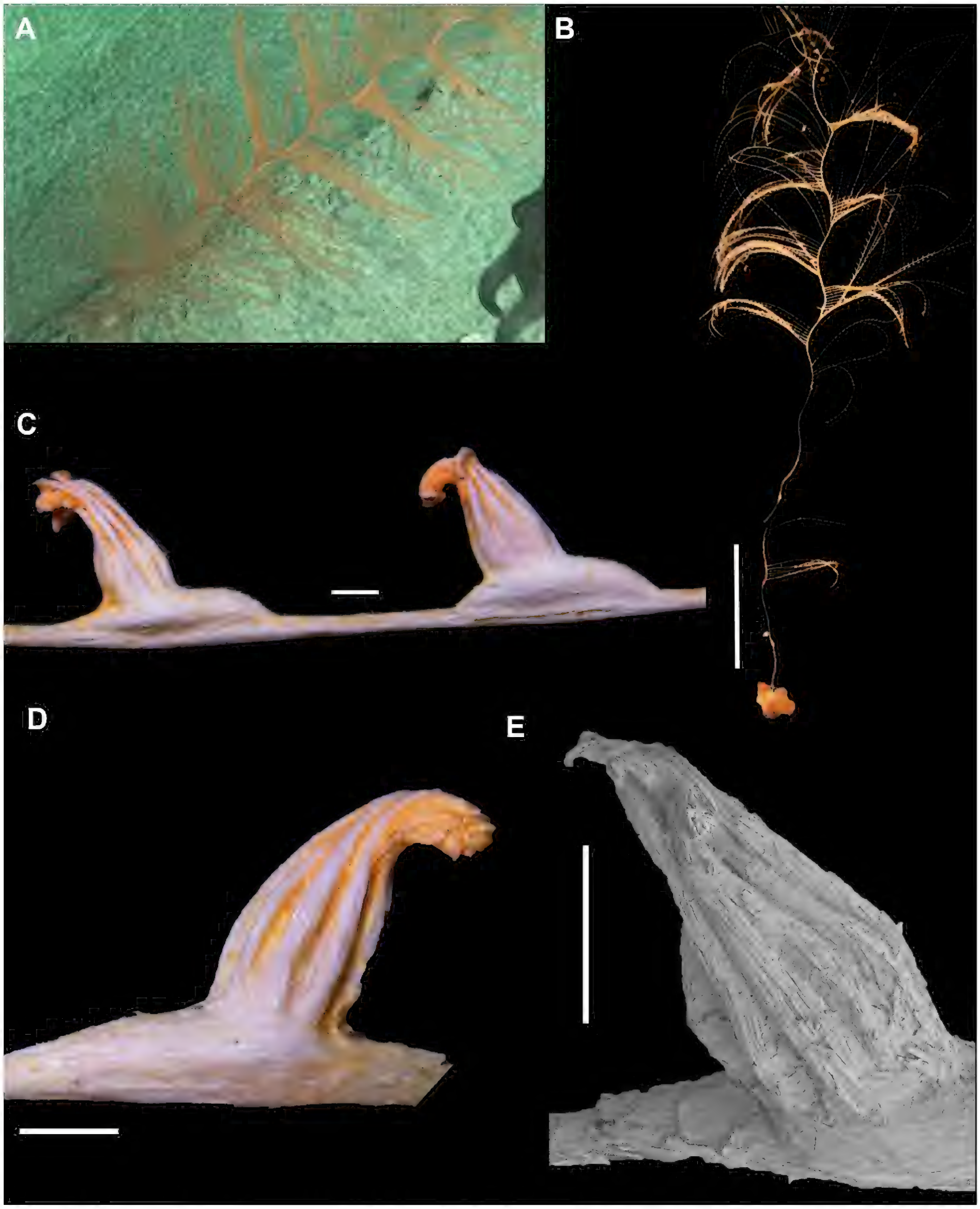

Figure 13. The external morphology of *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov. **A**, **B.** Specimen *in situ* and after collection; **C.** A part of the branch under a light microscope; **D.** Single polyp under a light microscope; **E.** Single polyp under SEM. Scale bars: 20 cm (**B**); 1 mm (**C, D**); 0.5 mm **E**.

Etymology. The species name *levisquama* is a compound noun derived from the Latin *levis* (smooth) and *squama* (scale), referring to the characteristic scales in the basal part of the polyp body wall, which are nearly smooth.

Distribution and habitat. Found from the Nineteyeast Ridge in the northern Indian Ocean with water depths of 2,073 m. Colony attached to a chalk substrate.

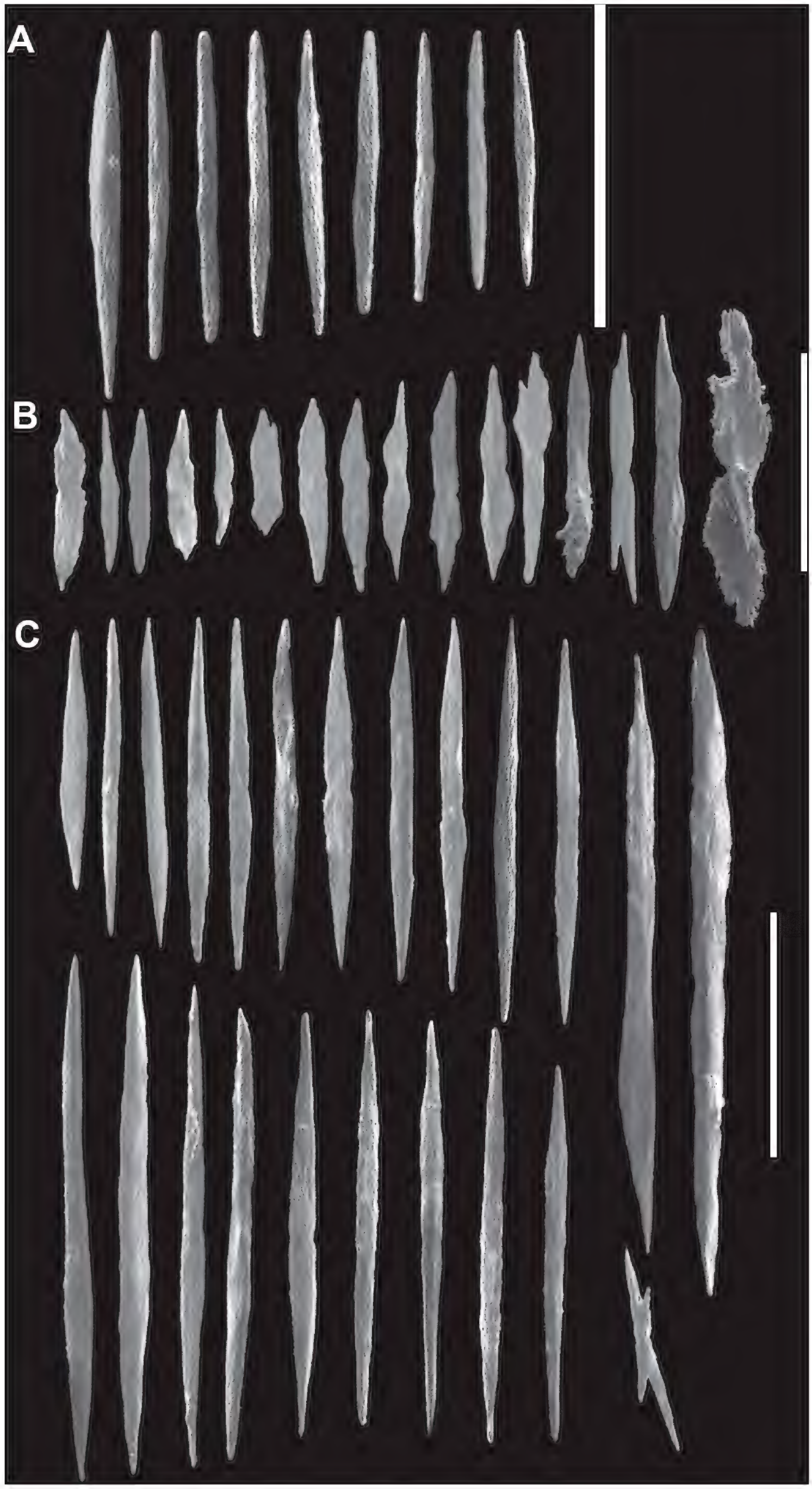

Figure 14. Sclerites of *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov. **A.** Sclerites in the tentacles; **B.** Sclerites in the basal part of the polyp body wall; **C.** Sclerites in the coenenchyme. Scale bars: 500 μm (**A**); 250 μm (**B**); 500 μm (**C**).

Remarks. *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov. resembles *I. squarrosa* and *I. magnispiralis* in having loosely coiled helices but differs from them in possessing slender needles in the tentacles with fine wartiness (vs. relatively stout needles and rods with dense warts in *I. squarrosa*; bluntly rounded rods in *I. magnispiralis*), as well as slender scales in the polyp body wall with sharp ends (vs. irregular needles and scales, occasionally with pointed ends in *I. squarrosa*; flattened to slightly rounded spindles in *I. magnispiralis*).

Genus *Metallogorgia* Versluys, 1902

Metallogorgia melanotrichos (Wright & Studer, 1889)

Figs 15–17

Dasygorgia melanotrichos Wright & Studer, 1889: 15, pl. IV, Fig. 3, pl. V, Fig. 5.

Metallogorgia melanotrichos: Versluys, 1902: 87.

Metallogorgia melanotrichos: Nutting, 1908: 593–594, pl. LI, Fig. 5.

Metallogorgia melanotrichos: Kükenthal, 1919: 503.

Metallogorgia melanotrichos: Pasternak, 1981: 51.

Metallogorgia melanotrichos: Xu et al., 2020: 14–19, Figs 7–10.

Material examined. FIO-IND72-JLBEN22401, Ninetyeast Ridge, 3.53°N, 90.44°E, 1,981 m, collected on 28 June 2022. FIO-IND72-JLBEN22310, Ninetyeast Ridge, 3.55°N, 90.41°E, 2,003 m, collected on 27 June 2022. FIO-IND72-JLBEN22301, Ninetyeast Ridge, 3.54°N, 90.41°E, 2,007 m. FIO-IND72-JLBEN22306, Ninetyeast Ridge, 3.55°N, 90.41°E, 2,003 m. FIO-IND72-JLBEN22510, Ninetyeast Ridge, 3.48°N, 90.44°E, 1,976 m, collected on 29 June 2022. FIO-IND72-JLBEN22605, Ninetyeast Ridge, 3.58°N, 90.16°E, 2,073 m, collected on 30 June 2022.

Description. ***Colony.*** Specimen FIO-IND72-JLBEN22401 tree-shaped with a long unbranched main stem and two large branches arising at the end of the stem, approximately 86 cm in height (Fig. 15A, C). The axis solid and flexible with black metallic luster. The angles of these large branches obtuse. Small branchlets subdivided dichotomously and sympodial on the plane of each large branch. A sea anemone Actinoscyphiidae sp. attached to the stem one-third of the base, and an *Ophiocreas oedipus*. attached to the branches. Other specimens comprise only part of the branches, almost all have *Ophiocreas oedipus* attachment (Fig. 15B, D–H).

Polyps. Polyps cylindrical, approximately 3 mm high, 1.2–1.7 mm wide, perpendicular to the branch (Fig. 15I, J). Polyps usually arranged one or two on each internode, up to 8 on the terminal branchlets, and absent on the main stem.

Sclerites. Rods in tentacles longitudinally arranged, a little flat with abundant fine warts and two rounded ends, some of them slightly curved or with irregular edges, measuring 19–369 μm long by 24–67 μm wide (Fig. 16A). Similar rods and elongate and thick scales in polyp body wall longitudinally arranged at the upper part, transversely or obliquely arranged at the basal part, measuring 174–365 μm long by 35–66 μm wide (Fig. 16B). Scales in coenenchyme arranged along the branch, thick and nearly smooth with two rounded ends, some of them with a medial constriction, occasionally crossed with irregular edges and sparse fine warts, measuring 123–273 μm long by 32–65 μm wide (Fig. 17).

Distribution and habitat. The type locality of *M. melanotrichos* is Ascension Island, South Atlantic, with a water depth of 778 m. It is recorded in the central Indo-Pacific Ocean, the western and central Pacific, and the Atlantic Ocean, with water depths ranging from 183 m to 2,265 m (Xu et al. 2020b). In this study, *M. melanotrichos* was collected from the Ninetyeast Ridge of the northern Indian Ocean, with depths of 1,976–2,073 m.

Remarks. Specimens of *M. melanotrichos* collected from the Indian Ocean match well with the original description. This species exhibits distinct ontogenetic variation: juveniles are characterized by a gracile stem with random lateral branching and the presence of polyps on the stem, while adults develop a robust monopodial stem with branching restricted to the distal end in a sympodial pattern and lack polyps on the stem. The collected specimens are identified as adult colonies based on their large size (86 cm in height) and the characteristic long, unbranched main stem. Additionally, nearly all *M. melanotrichos* samples were found to host the same ophiuroid species, *Ophiocreas oedipus*, consistent with specimens in the North Atlantic described by Mosher and Watling (2009), further supporting the host specificity of this epibiotic association between the two species.

Genetic distance and phylogenetic analyses

The alignments comprised 648 and 594 nucleotide positions for the *mtMutS* and *28S rDNA* regions, respectively. Based on the aligned *mtMutS* region (Suppl. material 1: table S2), the interspecific distances of *Chrysogorgia* range from 0 to 1.87%, and the intraspecific distances are in the range of 0–0.31%. The interspecific distances between *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. and its congeners are in the range of 0.46%–1.87%. In *Iridogorgia*, interspecific and intraspecific distances ranged from 0–1.56% and 0–0.32%, respectively. *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. was genetically identical to *I. curva*, *I. flexilis*, and *I. splendens* (0% divergence), while differing from other congeners by 0.15%–0.93%. Similarly, *I. levisquama* sp. nov. shared identical sequences with *I. squarrosa*, while exhibiting genetic distances of 0.15%–1.08% from the remaining species. The interspecific distances of *Parachrysogorgia* are in the range of 0–0.46%, and the intraspecific distance of *P. chryseis* was 0–0.15%. *Metallogorgia* exhibited interspecific and intraspecific distances of 0.15% and 0%, respectively. At the intergeneric level (Suppl. material 1: table S3), pairwise distances among the seven genera varied from 1.49% to 5.02%. The lowest divergence was observed between *Ramuligorgia* and *Iridogorgia* (1.49%), followed by *Chrysogorgia* and *Parachrysogorgia* (1.90%), whereas *Parachrysogorgia* and *Metallogorgia* showed the highest divergence (5.02%).

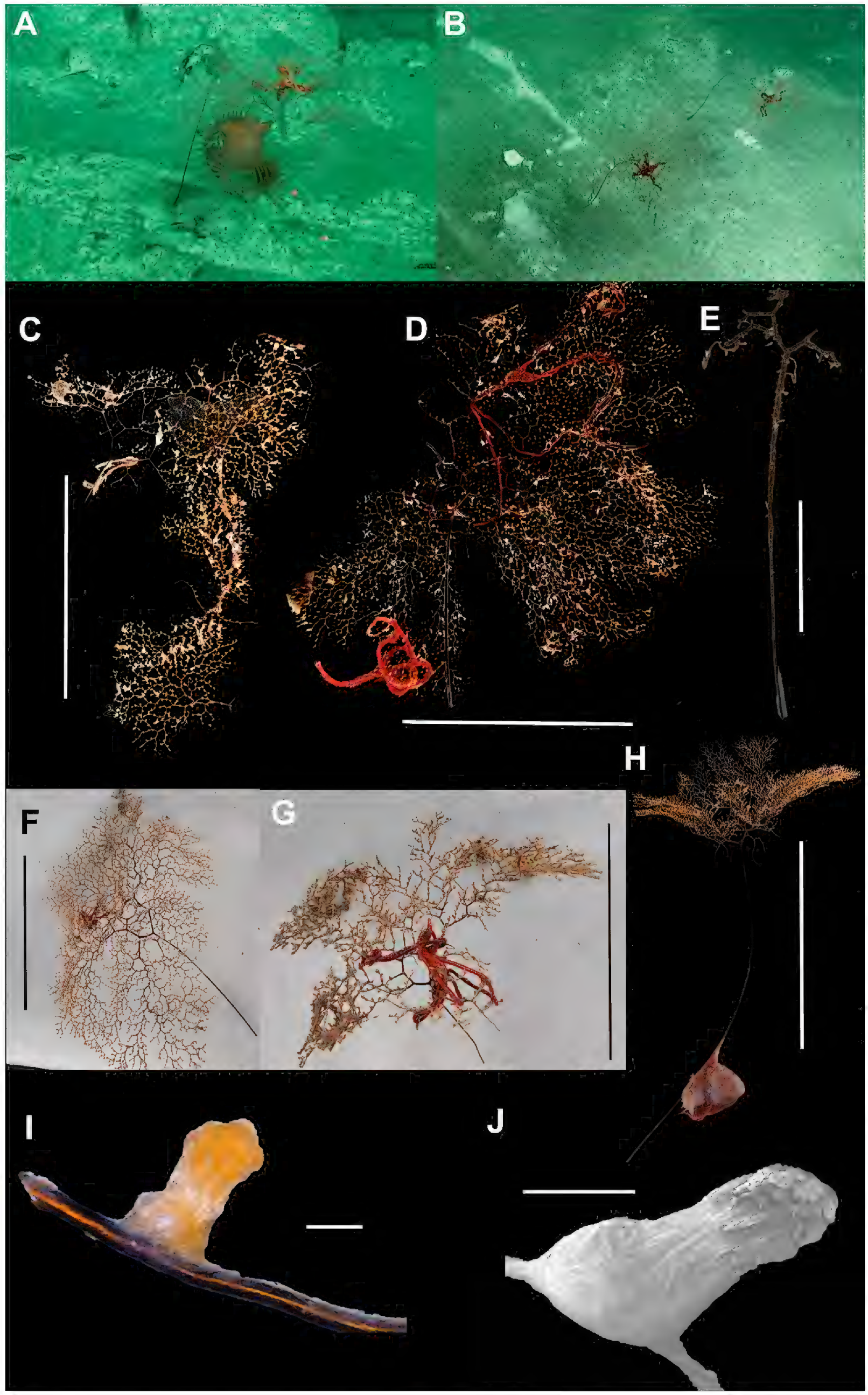

Figure 15. The external morphology of *Metallogorgia melanotrichos* (Wright & Studer, 1889). **A**, **B.** Specimens FIO-IND72-JLBEN22401 and FIO-IND72-JLBEN22310 *in situ*; **C–H.** Specimens FIO-IND72-JLBEN22301, FIO-IND72-JLBEN22310, FIO-IND72-JLBEN22306, FIO-IND72-JLBEN22510, FIO-IND72-JLBEN22605, and FIO-IND72-JLBEN22401 after collection; **I.** Single polyp under a light microscope; **J.** Single polyp under SEM. Scale bars: 20 cm (**C, D**); 1 mm (**I, J**).

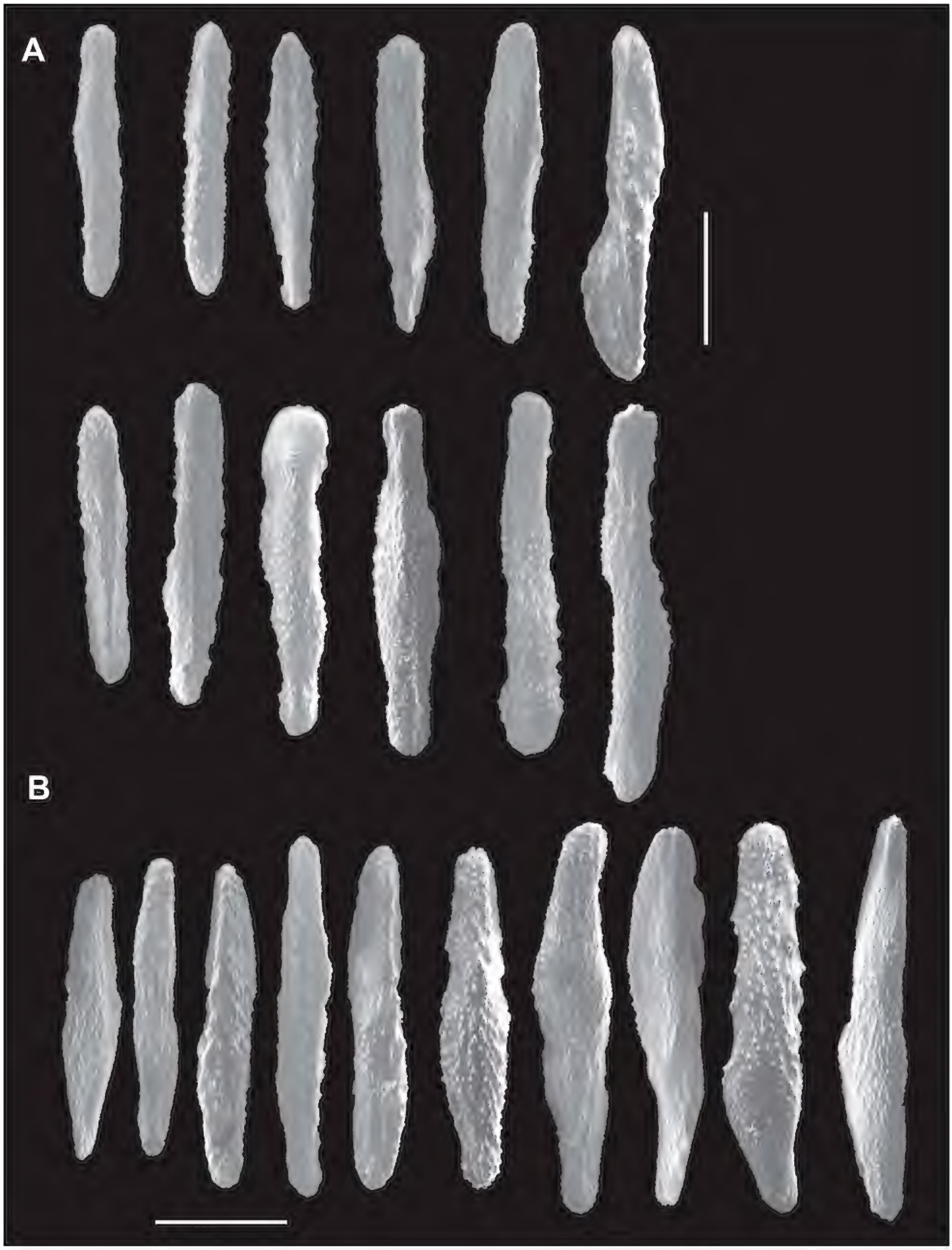

Figure 16. Sclerites of *Metallogorgia melanotrichos* (Wright & Studer, 1889), specimen FIO-IND72-JLBEN22401. **A.** Sclerites in the tentacles; **B.** Sclerites in the polyp body wall. Scale bars: 100 μm (**A, B**).

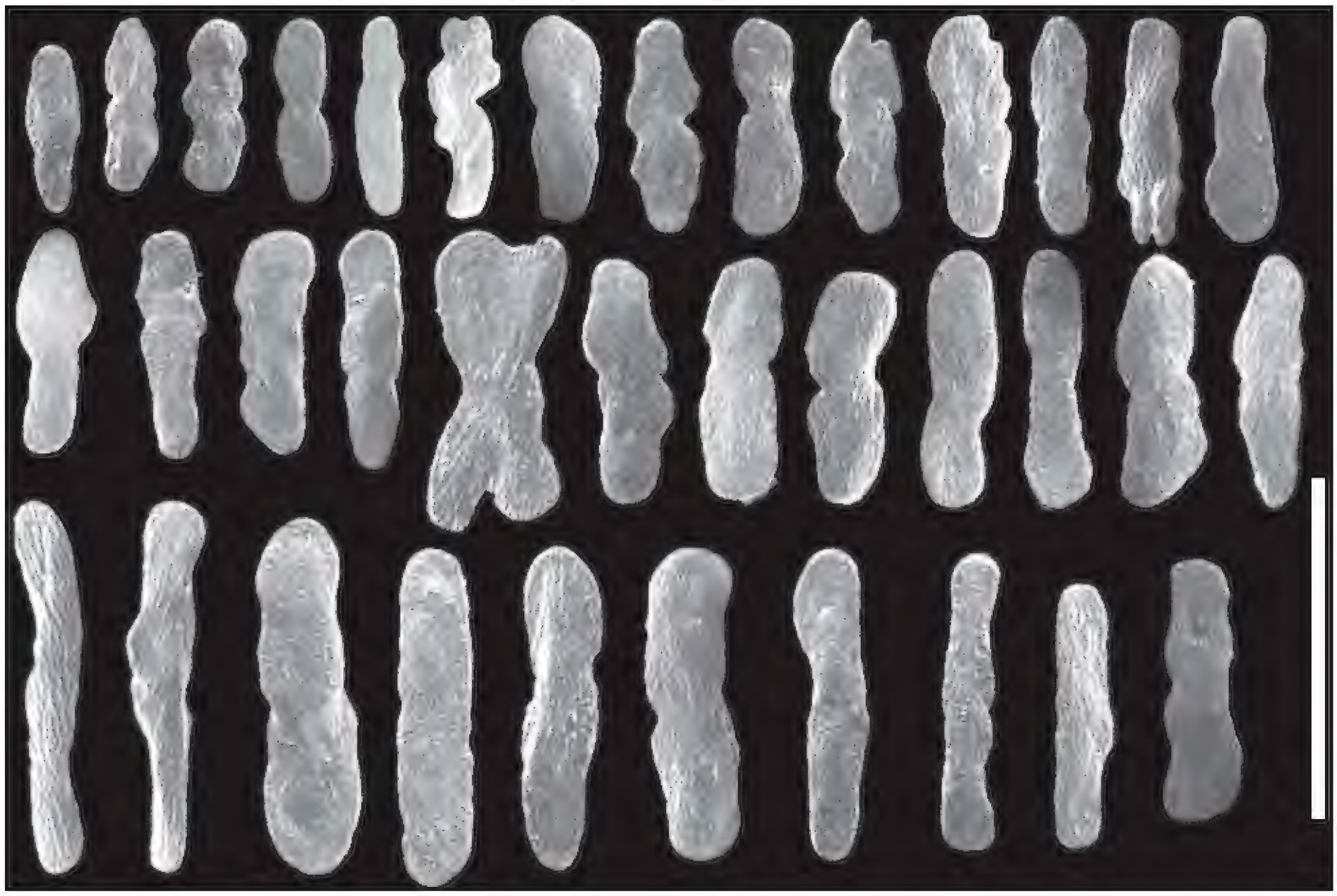

Figure 17. Scales in the coenenchyme of *Metallogorgia melanotrichos* (Wright & Studer, 1889), specimen FIO-IND72-JL-BEN22401. Scale bars: 250 μm.

Based on the *28S rDNA* region (Suppl. material 1: table S4), the interspecific distances of *Chrysogorgia* are in the range of 0.68%–13.49%, and the intraspecific distances are 0.17%–1.37%. *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. differed from other congeners by 1.53%–8.22%. For *Iridogorgia*, interspecific distances ranged from 0.17% to 6.72%, with no intraspecific variation detected. *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. and *I. levisquama* sp. nov. diverged from their congeners by 0.51%–5.22% and 1.18%–4.88%, respectively. In *Parachrysogorgia*, interspecific distances ranged from 0.68% to 3.93%, and the intraspecific distance of *P. chryseis* is 0–1.2%. No intraspecific variation was observed in *M. melanotrichos*. The intergeneric genetic distances among the seven genera based on *28S rDNA* sequences ranged from 3.17% to 17.60% (Suppl. material 1: table S5). The minimum genetic distance was observed between *Metallogorgia* and *Pseudochrysogorgia* (3.17%), while the maximum divergence occurred between *Parachrysogorgia* and *Iridogorgia* (17.60%).

The BI tree closely mirrors the ML tree and yielded congruent topologies for *mtMutS* and *28S rDNA* datasets, with support values of both methods displayed on a single ML tree (Figs 18, 19). Both *mtMutS* and *28S rDNA* trees strongly supported the monophyly of *Chrysogorgia*, *Iridogorgia*, *Parachrysogorgia*, and *Metallogorgia*. In the *mtMutS* tree, *C. pugnioides* sp. nov. formed a distinct lineage closely related to *C. ramificans* and *C. monticola* (ML = 93, BI = 1). *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. clustered with *I. splendens*, *I. curva*, and *I. flexilis*, but the support is not high. *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov. clustered with *I. squarrosa* with strong support (ML = 93, BI = 0.91). Additionally, specimens of *M. melanotrichos* and *P. chryseis* from the Indian Ocean clustered with their Pacific counterparts in well-supported clades (ML = 97, BI = 0.89, and ML = 91, respectively). In the *28S rDNA* trees, *C. pugnioides* sp. nov. was similarly resolved as a distinct branch, positioned as the sister group to a clade comprising *C. pinniformis*, *C. cylindrata*, *C. pendula*, and *C. acanthella* (ML = 96, BI = 0.93). *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. formed a well-supported clade (ML = 98, BI = 0.98). *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov. was recovered as a strongly supported independent lineage (ML = 82, BI = 0.94), sister to *I. squarrosa*. Furthermore, Indian Ocean specimens of *M. melanotrichos* and *P. chryseis* clustered with their respective Pacific conspecifics in well-supported clades (ML ≥ 98, BI ≥ 0.97).

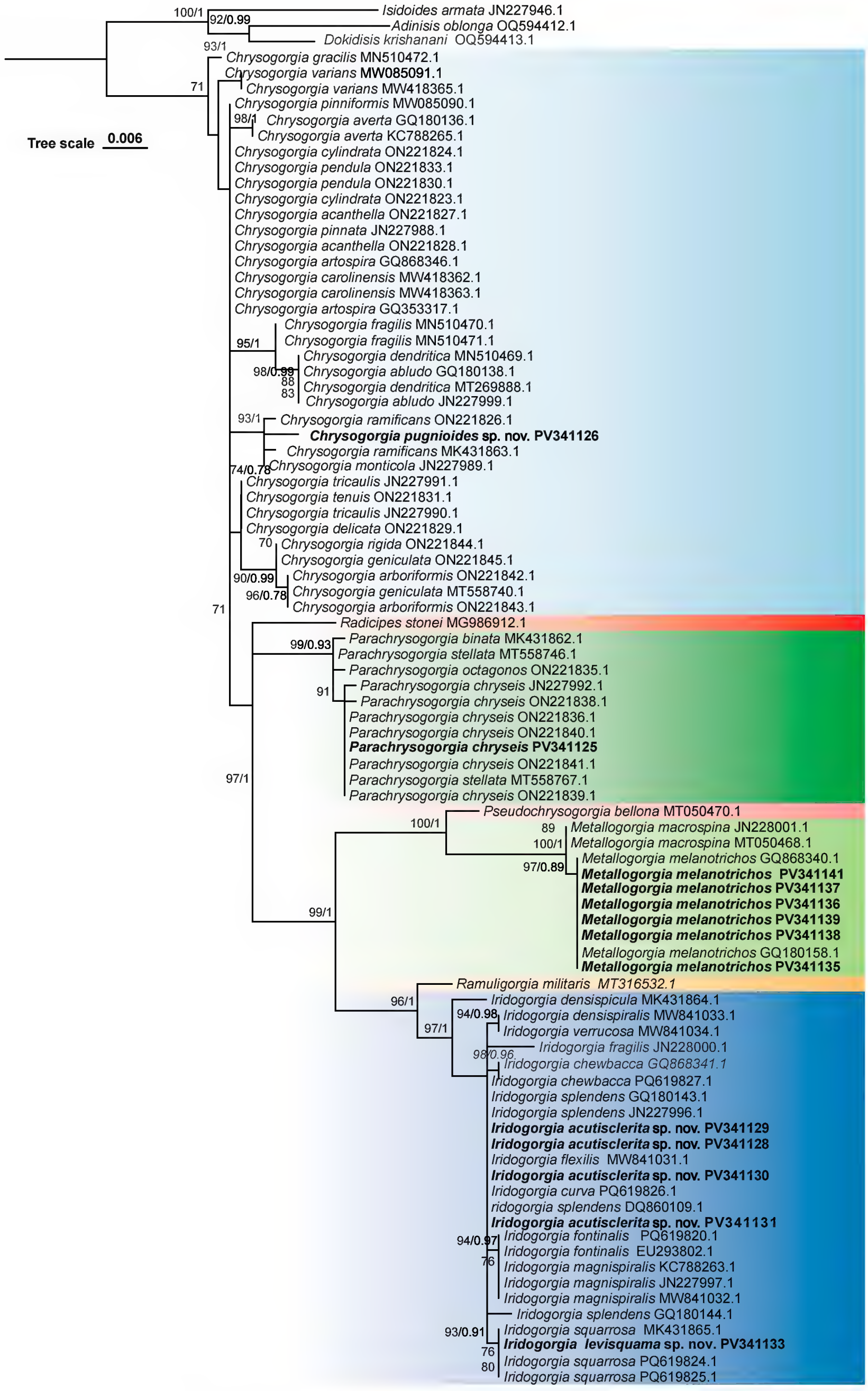

Figure 18. Maximum likelihood (ML) tree of Chrysogorgiidae constructed by *mtMutS*. The Bayesian inference (BI) tree is identical to the ML tree in topology. Node support is as follows: ML bootstrap/BI posterior probability. Nodes with ML bootstrap < 70% or BI posterior probability < 0.70 do not show support values. New sequences are in bold.

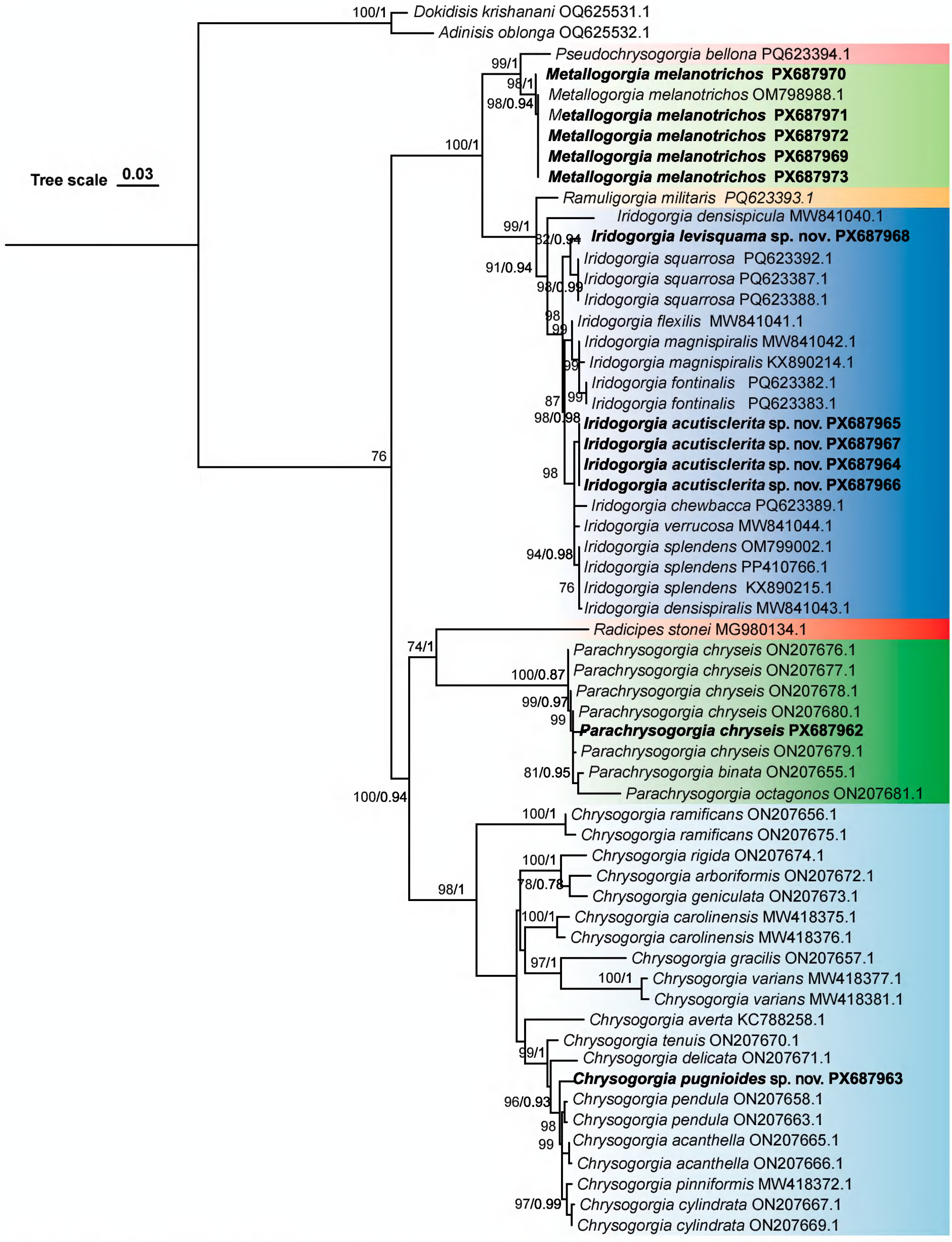

Figure 19. Maximum likelihood (ML) tree of Chrysogorgiidae constructed by *28S rDNA*. The Bayesian inference (BI) tree is identical to the ML tree in topology. Node support is as follows: ML bootstrap/BI posterior probability. Nodes with ML bootstrap < 70% or BI posterior probability < 0.70 do not show support values. New sequences are in bold.

Discussion

Systematics of the three new Chrysogorgiidae species

Three new species are placed within the genera *Chrysogorgia* and *Iridogorgia*, respectively, based on morphological and phylogenetic analyses. The phylogenetic topologies of *C. pugnioides* sp. nov. differ between the *mtMutS* and *28S rDNA* trees, which is primarily attributable to rate heterogeneity between mitochondrial and nuclear gene evolution in octocorals (Morrissey et al. 2024). In the *mtMutS* tree, *C. pugnioides* sp. nov. clustered with *C. ramificans* and *C. monticola* with low support values (ML < 70), failing to resolve the phylogenetic relationships. While in the *28S rDNA* tree, *C. pugnioides* sp. nov. formed a distinct, well-supported lineage (ML = 96, BI = 0.93) as the sister taxon to *C. pendula*, supporting the validity of this new species. Morphologically, *C. pugnioides* sp. nov. is similar to *C. ramificans* and *C. monticola* in colony form and branching sequence (1/3R or 2/5R) but differs by various sclerites in the polyp body wall. Specifically, *C. pugnioides* sp. nov. features flat spindles to elongate scales with toothed or irregular edges in the polyp body wall, distinctly different from the stout, regular rods and spindles in *C. ramificans* (Xu et al. 2019) and the flattened rods with blunt, pleated, and compressed tips in *C. monticola* (Cairns 2007). Thus, the morphological characteristics and phylogeny based on *28S rDNA* support the effectiveness of *C. pugnioides* sp. nov.

Iridogorgia acutisclerita Ge, Zhang & Xu, sp. nov. clustered with *I. splendens*, *I. curva*, and *I. flexilis* in the *mtMutS* phylogenetic tree but formed a distinct, well-supported clade in the *28S rDNA* phylogeny (ML = 98, BI = 0.98). Morphologically, *I. acutisclerita* sp. nov. shares a closely coiled colony form with *I. splendens* and *I. curva* but is easily distinguished by the presence of elongate scales and flat needles with two pointed ends in the polyp body wall (vs. absence of scales in both congeners, with rods and needles being thick/irregular in *I. splendens* and slender/smooth in *I. curva*) (Xu et al. 2025). *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov. is genetically related to *I. flexilis* but morphologically different from the latter by a closely coiled colony (vs. loosely coiled with a long unbranched stem), sparse rods in the tentacles (vs. abundant rods), and slender, regular needles and scales with two pointed ends in the polyp body wall (vs. stout, thick, and irregular spindles/scales) (Xu et al. 2021).

Iridogorgia levisquama Ge, Zhang & Xu, sp. nov. showed a close affinity to *I. squarrosa* in the *mtMutS* analysis but was resolved as a separate lineage in the *28S rDNA* phylogeny with moderate support (ML = 82, BI = 0.94). Morphologically, as mentioned above, *I. levisquama* sp. nov. resembles *I. squarrosa* in a loosely coiled colony, but it differs primarily by sclerite morphology. *Iridogorgia squarrosa*, described by Xu et al. (2025), possesses needles and rods with small warts in the tentacles, thick needles and elongate scales with various shapes and fine warts or large sculpture in the polyp body wall, and slender needles in the coenenchyme. The sclerites of *I. levisquama* sp. nov. are smoother (needles and rods in the tentacles with fine warts, scales in the polyp body wall nearly smooth and lacking large sculptures) and sharper at both ends.

The biogeographic distribution of Chrysogorgiidae in the Indian Ocean

Five gorgonian species, including three new species, were found in the Carlsberg Ridge and the Ninetyeast Ridge in the northern Indian Ocean, suggesting that the Indian Ocean Ridge may represent an overlooked diversity hotspot for Chrysogorgiidae. Currently, records of Chrysogorgiidae species in the Indian Ocean are mainly concentrated along the western and northern shelf margins and the Indo-Pacific transition zone. *Chrysogorgia* dominates the chrysogorgiid fauna in the Indian Ocean, primarily distributed in the Bay of Bengal, the Andaman Sea, and the Indo-Pacific region, including some endemic species such as *C. indica* and *C. irregularis* (Thomson et al. 1906). *Parachrysogorgia octagono* and the *Metallogorgia*, including *M. macrospina* and *M. melanotrichos*, were recorded from the Indo-Pacific (Xu et al. 2020b, 2023). *Radicipes aureus* is mainly recorded on the western Indian Ocean slope (Cordeiro et al. 2017).

Two new *Iridogorgia* species (*I. acutisclerita* sp. nov. and *I. levisquama* sp. nov.) are the first confirmed taxonomic records of this genus in the Indian Ocean. *Iridogorgia* has previously recorded 14 effective species, with three high-diversity regions: the tropical western Pacific (10 species), the waters around Hawaii (five species), and the Northwest Atlantic (five species) (Xu et al. 2025). Although recent ROV surveys have documented *Iridogorgia* in the Perth Canyon, southeastern Indian Ocean (Trotter et al. 2019), these observations have not yet formally described species. Consequently, the taxonomic establishment of these two new species validates the occurrence of *Iridogorgia* in the northern Indian Ocean, significantly expanding its known biogeographic range beyond the traditional diversity centers in the Pacific and Atlantic Oceans.

Conclusion

Three new species of the family Chrysogorgiidae, *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov., *Iridogorgia acutisclerita* Ge, Zhang & Xu, sp. nov., and *Iridogorgia levisquama* Ge, Zhang & Xu, sp. nov., together with two known species, *Parachrysogorgia chryseis* and *Metallogorgia melanotrichos*, were described from the northern Indian Ocean in this study. Morphological and molecular phylogenetic analyses support the establishment of the three new species. *Chrysogorgia pugnioides* Ge, Hu and Xu, sp. nov. and *P. chryseis* were collected from the

Carlsberg Ridge, whereas *I. acutisclerita* sp. nov., *I. levisquama* sp. nov., and *M. melanotrichos* were discovered on the Ninetyeast Ridge. This study expands our knowledge of Chrysogorgiidae diversity in the Indian Ocean and provides a foundation for future biogeographic and evolutionary studies of deep-sea octocorals in this region.

Acknowledgments

We acknowledge the support from the National Key R&D Program of China (No. 2023YFC2812903) and the Digital Deep-sea Typical Habitats Program of the China Deep Ocean Affairs Administration. We also gratefully acknowledge the International Seabed Authority (ISA)'s Sustainable Seabed Knowledge Initiative: One Thousand Reasons Campaign, with a voluntary contribution by the Government of Ireland to the ISA Partnership Fund. We thank the scientists and crews of the R/V *Shenhai Yihao* and submersible pilots of HOV *Jiaolong* for their assistance with sample collection during the DY72 cruise.

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Supplementary material 1

Supplementary tables

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Data type: xlsx

Explanation note: **table S1.** The sequences used in this study. New sequences are in bold. **table S2.** Interspecific and intraspecific distances at mtMutS of Chrysogorgia species, Parachrysogorgia Iridogorgia and Metallogorgia. measured by p-distance based on mtMutS (%). **table S3.** Intergeneric genetic distance of Chrysogorgiidae measured by p-distance based on mtMutS. **table S4.** Interspecific and intraspecific distances of Chrysogorgia species, Parachrysogorgia Iridogorgia and Metallogorgia measured by p-distance based on 28S rDNA (%). **table S5.** Intergeneric genetic distance of Chrysogorgiidae measured by p-distance based on 28S rDNA.

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